8-15-2018

Plant and Soil Carbon Responses to Invasive Typha Management in Great Lakes Coastal Wetlands

Olivia Johnson
olivia.2.johnson@uconn.edu

Plant and Soil Carbon Responses to Invasive *Typha* Management in Great Lakes Coastal Wetlands

Olivia Fayne Johnson

B.S., DePaul University, 2016

A Thesis

Submitted in Partial Fulfillment of the

Requirements for the degree of

Master of Science

at

University of Connecticut

2018

APPROVAL PAGE

Masters of Science Thesis

Plant and Soil Carbon Responses to Invasive *Typha* Management in Great Lakes Coastal Wetlands

Presented by

Olivia Fayne Johnson, B.S.

Major Advisor _____

Beth A. Lawrence

Associate Advisor _____

John C. Clausen

Associate Advisor _____

Ashley M. Helton

University of Connecticut

2018

Acknowledgments

Thank you to my major advisor, Dr. Beth Lawrence, for introducing me to wetland ecology, offering patience and motivation, and guiding me toward a career that combines my passion, skills, and values. From DePaul University greenhouse to Cheboygan marsh to University of Connecticut classroom, I appreciate the conversations, objectives, victories, challenges, and growth throughout the last three years.

This work was financially supported by the U.S. Environmental Protection Agency's Great Lakes Restoration Initiative. I'm grateful for Shane Lishawa, Brendan Carson, Andrew Monks, and other researchers of "Team Typha" who taught me sampling techniques, talked through statistical inquiries, and most importantly modeled collaboration toward care of Great Lakes resources. Thank you to the staff and scientists at University of Michigan Biological Station, especially Karrie Slavik for coordinating summer funding, and Timothy Veverica for answering my many analytical chemistry questions. Additional funding came from UConn's College of Agriculture, Health, and Natural Resources. I'm grateful for the educational leaders and professional role models found in the Department of Natural Resources and the Environment, especially Dr. John Volin, Dr. Jason Vokoun, Dr. John Clausen, and Dr. Ashley Helton.

Dr. Rose Martin and Dr. Serena Moseman-Valtierra provided R-script to calculate gas flux from *in-situ* chamber measurements. Gary Ulatowksi, Dr. Brian Ohsowski, and Dr. Lucas Nathan assisted with creating supplies and writing R-script for carbon mineralization analysis, and shared countless dialogues of moral support during my young scientific endeavors. I sincerely appreciate the field hours, lab work, and friendship from Moriah Young, Matt Connors, Sammy Keyport, Sean Khan Ooi, Matt Unitis, Kate Wellons, Nicole Spehn, Mary Donato, Alaina Bisson, Sammy Walker, and Aidan Barry. Finally thank you to my, mom, brother, and extended family for all the love, music, questions, laughter, and encouragement throughout this process.

Table of Contents

List of Tables

Invasive *Typha* control techniques alter freshwater wetland surface carbon pools and plant-mediated carbon fluxes

How do invasive *Typha* management treatments alter plant-soil feedbacks in northern Great Lakes coastal wetlands?

List of Figures

Invasive *Typha* control techniques alter freshwater wetland surface carbon pools and plant-mediated carbon fluxes

How do invasive *Typha* management treatments alter plant-soil feedbacks in northern Great Lakes coastal wetlands?

Abstract

We quantified how control of a ubiquitous Great Lakes region invasive (*Typha* × *glauca*) shifts plant-mediated C cycling and belowground dynamics. Two field experiments implemented large scale treatment plots (~1-ha to 3-ha) of harvesting (i.e., cut above water surface, removed biomass), crushing (i.e., ran over biomass), and creating connectivity channels (i.e., cut at the soil surface, create open-water within *Typha*-dominated stands). In one experiment, we observed immediate C release via gas flux and aqueous C; harvesting and crushing caused net emission of carbon dioxide (CO_2), and crush increased dissolved organic carbon in the surface water and particulate organic carbon in soil pore water. Within one year, all treated *Typha* stands regrew with reduced stem height, which increased light penetration to the water surface. Harvested stands had greater CO_2 uptake relative to un-manipulated controls, but also had greater methane (CH_4) emissions, decreasing the wetland's capacity to sequester C. In another experiment, *Typha* remained absent from channels, leading to greater light transmission through the water column to the soil surface, and channels had increased soil pore water availability of phosphorus and potassium. CO_2 and CH_4 soil production rates were positively related to iron availability, so the interaction between carbon turnover and soil redox may counteract the effect of treatment. Our study suggests mechanical invasive macrophyte control can alter aboveground structure, carbon flux, and soil availability of certain nutrients, and these factors should be included in evaluation of management tradeoffs (i.e., plant diversity and wildlife habitat vs. carbon mitigation and nutrient removal).

Invasive *Typha* control techniques alter freshwater wetland surface carbon pools and plant-mediated carbon fluxes

Introduction

Globally, wetlands provide critical carbon storage (Mitsch et al. 2013, Bridgham et al. 2006). High primary productivity of wetland vegetation promotes carbon dioxide (CO_2) uptake, and waterlogged soils decrease aerobic decomposition, resulting in the accumulation of organic rich soils. Simultaneously, these conditions promote anaerobic production of methane (CH_4), a significant carbon source with 28 times more climate warming potential than CO_2 over 100 years (Myhre et al. 2013). The carbon balances of wetlands are increasingly relevant to management efforts, as wetland carbon sequestration contributes to climate regulation, and plant-soil-water carbon cycling is important to the overall functional diversity of a wetland (Mitsch et al. 2013, Bennett et al. 2009). Wetlands face various stressors including nutrient loading and macrophyte invasion; these systems are focal habitats for managers aiming to increase plant diversity and wildlife habitat or to optimize nutrient retention and stormwater abatement, yet carbon storage is not often a management priority (Sierszen et al. 2012).

One of the most prevalent issues facing wetland practitioners is invasion of monotypic macrophytes. Across North America, hybrid cattail (*Typha x glauca*, hereafter *Typha*), common reed (*Phragmites australis*), and reed canary grass (*Phalaris arundinacea*) create dense and tall vegetative stands that out-compete native species and degrade wetland quality (Zedler & Kercher 2005). Effective invasive species control may require repeated action and monitoring, especially where environmental conditions (i.e. surrounding land-use, water level) prevent re-establishment of native species (Quirion et al. 2018). Control of *P. australis* in the U.S. alone costs almost 5 million dollars per year, much of which is spent on herbicide application (Martin

& Blossey 2013), and there is increasing consensus such chemical methods are not viable long-term solutions (Quirion et al. 2018). In an era of growing conservation concerns and smaller budgets, there is a need to identify ecologically meaningful and cost-effective management efforts.

Non-native plants often sustain dominance via feedbacks such as altering nutrient cycling and biomass accumulation (Galatowitsch et al. 1999, Suding et al. 2004, Larkin et al. 2012), so targeting these feedbacks is essential to improving wetland management outcomes. For example, mechanical control methods have the potential to disrupt litter accumulation, a main mechanism by which invasive *Typha* and *Phragmites* maintain their dense monocultures (Farrer & Goldberg 2009, Vaccaro et al. 2009, Holdredge & Bertness 2010). These techniques may restore structural complexity, catalyze regrowth from the native seed bank, increase light penetration, and lead to abiotic and biotic feedbacks that sustain a less-invaded state (Lishawa et al. 2015, Zedler 2009).

Multiple mechanical techniques can reduce invasive plant dominance. Crushing (i.e., running over with an aquatic track vehicle) invasive biomass is an appealing technique because it is relatively low cost and it immediately reduces dense stands of vegetation (Beule 1979). *Typha* dominance, stem density and height decreased at a freshwater wetland in Costa Rica one year after a single treatment of "fangueo," which consisted of shredding biomass with a metal paddle wheel on aquatic tractor, and is analogous to crushing biomass (Osland et al. 2011). Harvesting (i.e., mowing and removing) invasive biomass may promote a range of ecosystem services by increasing plant diversity, removing nutrient-dense plant tissues, and providing substrates that can be used as soil amendments or as bioenergy feedstocks (Jakubowski et al. 2010, Carson et al. 2018). At a northern Great Lakes coastal wetland, one-time harvest

decreased *Typha* dominance and litter biomass for two years (Lishawa et al. 2015), with effects persisting four years post-treatment (Keyport et al. *in press*). *Phragmites australis* aboveground biomass on the periphery of an Italian lake decreased two years after repeated harvest (Fogli et al. 2014), while mowing increased clonal spread and specific leaf area of vegetation in a sedge- and moss- dominated fen in Poland (Kotowski et al. 2013). Thus, current literature suggests mechanical disturbance can shift plant biomass allocation, decreasing aboveground biomass in most cases. Still, it is unclear how this biomass shift may alter rates of primary production, which influence wetland CO_2 uptake and CH_4 emissions. While plant biomass and diversity are vital elements of ecosystem response to management, assessment is incomplete without considering plant-mediated carbon pools and fluxes.

Scientists and land managers need to apply understanding of carbon cycling to assessment of wetland management efforts. In North America, freshwater wetlands are responsible for 45% of CO_2 uptake, but contribute 54% of CH_4 emissions (Bridgham et al. 2006). Vegetation indirectly influences the gaseous products of microbial activity by mediating the quantity and quality of carbon substrates available for heterotrophic processes (i.e., root exudates; Kayranli et al. 2010). Plants photosynthesize and directly assimilate CO_2 to organic carbon that is allocated to biomass growth or stored in rhizomes (Kayranli et al. 2010, Ehrenfeld et al. 2005). Further, wetland plants release carbon via internal gas transport through aerenchymatous tissue; by diffusion across concentration gradients, and by mass flow across pressure gradients. These mechanisms transport oxygen down to the rhizosphere and soil gases (i.e., CH_4) up to the atmosphere (Grosse et al. 1996, Laanbroek 2010, Carmichael et al. 2014). It is necessary to understand how management efforts affect wetland carbon cycling, in order to

consider trade-offs among carbon storage and other ecosystem services, such as biodiversity and water quality (Peralta et al. 2018, Bennett et al. 2009, Rodríguez et al. 2006).

While evidence indicates that biomass removal has no short-term effect (one-month) on soil organic matter or soil nutrient content (nitrogen, carbon, phosphorus; Osland et al. 2011, Kandel et al. 2013), extended monitoring is needed to investigate biogeochemical responses over time. Aboveground clipping had no immediate effect on CH_4 emissions from wetland mesocosms, perhaps because soil nutrient content can reduce CH_4 emissions and potentially counteract harvest effects (e.g., ammonia can inhibit CH_4- oxidizing bacteria; Rietl et al. 2017, Bodelier & Laanbroek 2004). In contrast, increased *in-situ* CH_4 emissions from stems grazed by waterfowl have been observed (Dingemans et al. 2011, Winton & Richardson 2017), as CH_4 can directly diffuse from anoxic soil to the atmosphere via cut stems. In a European peatland, harvest of *Phalaris* led to decreased soil CH_4 emissions within three months of treatment, but did not affect aboveground biomass or CO_2 uptake relative to un-disturbed references (Kandel et al. 2013). These divergent trends in carbon gas flux may be due to differences in carbon pools, and motivated our current study of plant biomass metrics, surface and soil water carbon content (particulate- and dissolved organic carbon; POC, DOC, and acetate, a common substrate for methane production), and *in-situ* real-time gas measurements.

One limitation identified in current wetland invasive plant control research is that the spatial and temporal scales of inquiry are not broad enough to assess comprehensive ecosystem response (Petersen et al. 2003, Wagner et al. 2008, Vaughn 2010). We leveraged a large-scale, multi-year restoration experiment in northern Michigan (USA) over more relevant spatial and temporal scales to quantify how mechanical invasive plant management techniques alter wetland plant-mediated carbon cycling. Treatments targeting invasive *Typha* were implemented

seasonally for three years, and we measured carbon-related parameters to assess both longer-term (> one–year post treatment*)* and immediate (< one-month post treatment) effects. We hypothesized that:

1) Longer-term *Typha* biomass allocation would shift in response to treatment, increasing belowground to aboveground biomass ratios, due to decreased live stems.

2) Harvesting invasive aboveground biomass would increase immediate CH_4 emissions via cut stems, but decrease longer-term carbon inputs (plant biomass, aqueous C), decreasing CO_2 and CH_4 emissions over longer-term.

3) Invasive plant crushing would increase immediate carbon (plant biomass, aqueous C) availability for heterotrophic processes and increase CO_2 and CH_4 emissions, but this pulse might not persist over longer-term.

Methods

Experimental design- Typha has been a management concern in the northern Great Lakes region for over 20 years, and our study site has been a focal point of research investigating the impacts of *Typha* invasion, as *Typha* dominates (> 99%) the aboveground biomass (Tuchman et al. 2009, Larkin et al. 2012). Cheboygan marsh is a Great Lakes lacustrine open-embayment wetland (palustrine emergent marsh) on northern Lake Huron (lat 45°39'N, long 84°28'W). This wetland is a benchmark site in the Great Lakes coastal wetland monitoring project (Uzarski et al. 2017), and is a model freshwater coastal system to investigate potential restoration strategies and their outcomes (Lishawa et al. 2015, Berke 2017, Keyport et al. *in press*).

In 2015, 60 m x 60 m plots were established and randomly assigned management technique treatments (n = 5); "annual harvest" (in mid-July with a low psi Loglogic Softrak, Devon, UK), "multi-harvest" (in mid-July and early September with Softrak), "crush" (in mid-

July with low psi amphibious vehicle, Ontario Drive & Gear Limited Argo, Ontario, CA), and *Typha*-dominated, un-manipulated "control." Treatments were repeated during each growing season during 2015- 2017. The present study focuses on the multi-harvest (hereafter "harvest"), crush, and control stands (Fig. 1). We collected carbon-related metrics during the 2016 and 2017 growing seasons (Table 1).

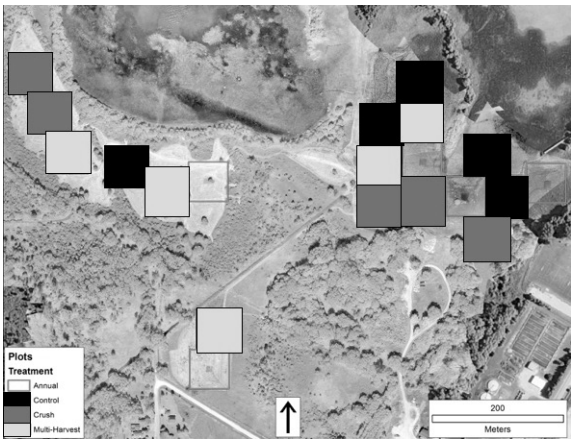


Figure 1. Experimental design of invasive *Typha* management treatments at Cheboygan marsh; 60 m x 60 m plots were randomly assigned and implemented treatments in 2015, and repeatedly treated in 2016 and 2017. The present study sampled control (black), crush (dark grey), and multi-harvest (hereafter harvest; light grey) plots. The annual plots were not included in the present study.

Table 1. Mechanical treatments and water, plant, and abiotic sampling timeline.

	2015			**2016**				**2017**		
	Mid JUL	Early SEPT	Early JUL	Mid JUL	Early AUG	Early SEPT	Early JUL	Mid JUL	Early AUG	Early SEPT
Experimental Treatment										
Harvest	X	X		X		X		X		X
Crush	X			X				X		
Sampling Parameter										
Surface & pore water carbon			X		X					
Litter mass			X							
Stem density and height			X				X		X	
Root biomass			X							
Rhizome biomass			X							
Water level			X		X		X		X	
Light transmission							X		X	
Gas flux (CO_2, CH_4)							X		X	

Field Sampling – For plant and water sampling, we established five subplots within each 60 m x 60 m plot; one placed in the center and four equidistant between center and corners, to minimize edge effects. In July 2016, we collected litter by hand (all standing dead and horizontal detritus within 25 cm x 25 cm quadrats), and belowground biomass using a shovel (25 cm x 25 cm area to ~12 cm depth) from three (randomly determined) of the five subplots. The only exception was our first sampling plot, a harvest plot where we sampled from four subplots. We also measured stem height and water depth from the soil surface using a meter stick, and counted the number of stems (within 1 m^2 quadrats) in the same subplots. After washing away soil and sediment from belowground biomass with a garden hose over 2-mm mesh screens, we separated roots from rhizomes. All biomass was dried at 60°C for at least 72 hours and weighed, then cut into small fragments (~2 cm), pulverized in a ball mill (400 rpm), and stored in a desiccator until further analysis. Stem height and density, and water depth were recorded in 1 m^2 plots in July 2017 at all five subplots.

In July and August 2016, we collected surface (at air-water interface) and pore (10 cm below soil surface) water. For DOC and POC analysis, we sampled surface and pore water at three, randomly determined subplots, and for acetate analysis we sampled pore water from all five subplots. All water samples were stored in 50-ml acid washed centrifuge tubes. Surface water was collected into tubes by immersing it directly below the water surface and capping it. Pore water samples were drawn using a nylon syringe and tubing from 2.54 cm diameter slotted PVC wells that were wrapped in fiberglass screening and were installed at least two days prior to sampling. We flushed the syringe three times to draw a well-mixed sample, and rinsed the syringe between samples. Surface water sampling for DOC was repeated in July 2017. All water samples were stored frozen until analysis.

In July and August 2017, we measured real-time CO_2 and CH_4 concentrations using a PVC-framed chamber (0.25 m x 0.25 m area x 2 m tall) wrapped with transparent UV-resistant PVC film, with two internal fans to circulate air, a vent tube, and sampling port (Holland et al. 1999). We sampled at subplots near three of the four corners of the 60 m x 60 m plots, because we transported our equipment on a large-tracked aquatic vehicle that would significantly disturb the vegetation in these long-term plots. We drove the vehicle ~5 m into the interior of each plot and used a boardwalk to walk to gas sampling subplots, ~7 m from plot edges, minimizing soil disturbance during gas sampling. At each deployment, we attached an I-button temperature sensor (Maxim Integrated, California, USA) to the inside of the chamber to record air temperature, and sealed the chamber to the water surface over the plants using a floating foam base. We connected the chamber to a Picarro G2201-i cavity ring-down spectrometer (Picarro, California, USA) via Teflon tubing from the sampling port. A vacuum pump (~30 ml/min) drew air into the instrument during a 10-minute incubation. At the time of gas sampling, we measured photosynthetically active radiation (PAR) 2.35 m above the soil surface and at the water surface with a quantum sensor (Li-Cor LI-189), and we recorded air and water temperatures adjacent to the chamber.

Lab processing- Water samples were passed through pre-combusted 0.45-nm glass fiber filters, and the filtrate was analyzed for DOC on a Shimadzu Total Organic Carbon Analyzer (at University of Connecticut's Center for Environmental Science and Engineering analytical lab in 2016 and at UConn's Department of Environmental Engineering analytical lab in 2017) using EPA Method 415.1. To analyze POC, the remaining particulate matter on the filter was dried for 3 days at 105°C, weighed, combusted at 500°C for four hours, and re-weighed to determine total organic content. Total organic content was converted to POC using the conventional Von

Bemmelen factor of 0.58. Acetate content was analyzed on a Dionex high-performance ion chromatograph at the University of Michigan Biological Station analytical lab in 2016. Pulverized litter, roots, and rhizomes were analyzed for C:N content on a Costech Elemental Analyzer in 2016.

Calculations and statistical analyses- We calculated total live biomass using a site-specific allometric equation that exponentially relates *Typha* stem height to biomass, and scaled all our dry biomass data to grams per square meter. We calculated the belowground to aboveground ratio by dividing the total belowground biomass (roots + rhizomes) by the living aboveground biomass (*Typha* stems), and did not include litter in this ratio because we were interested in differences in allocation to living tissue.

For gas flux calculations, measurements that indicated chamber error, such as chamber tipping during incubation or elevated initial concentrations due to ebullition, were excluded from analysis; 54 chamber incubations, 3% of CO_2 rates and 20% of CH_4 rates were excluded due to chamber error. We calculated gas flux rate as the linear change in concentration over time, corrected for chamber temperature, atmospheric pressure, and chamber volume, based on the ideal gas law (R-script shared by S. Moseman-Valtierra and R. Martin, personal communication). Correlation tests were used to test whether the slope of gas concentration over time differed from zero; p-values > 0.05 were concluded to have zero flux rates. Any non-linear change (R^2 value < 0.8) was re-calculated using only the half of the incubation (linear change over first five minutes), and excluded from analysis if re-calculation did not improve fit; of 54 chamber incubations, 2% of CO_2 flux rates and 22% of CH_4 flux rates were excluded due to non-linearity. We calculated percent light penetration by dividing PAR at the water surface by PAR 2.35 m above the substrate (soil) surface and multiplying by 100.

Within each growing season, all data were analyzed for treatment effects with linear mixed effects models (*lmertest* package in R version 3.4.1), which included plot as a random factor to account for repeated measures and spatial variation. In addition to treatment (control, crush, and harvest) and sampling date (pre/post treatment within each growing season), we included water depth as a covariate because dissolved compounds may be diluted by deeper water, aboveground biomass may grow taller in deeper water, and water depth may affect gas diffusion. For gas flux responses, we also included above-canopy PAR as a covariate to account for ambient variation in light availability that may affect photosynthesis and stomatal conductance. Data were log-10 transformed when necessary to meet parametric and residual assumptions of linear mixed effects models.

Biomass data and plant carbon data were analyzed at the subplot level to maintain the highest spatial resolution possible, and were analyzed individually to test for the effect of treatment, surface water depth (measured at same subplot of biomass sampling) and their interaction. Aqueous carbon (DOC, POC, and acetate) data were aggregated to the plot level in order to include plot-level water depth (average of subplot data taken at biomass subplots) as a covariate in analysis. Aqueous C data were analyzed to test for effect of treatment, and its interaction with date and water depth. Similar to biomass data, because we collected all our parameters of interest simultaneously at the subplot level, gas flux data were left at this higher resolution, and were analyzed by identity (CO_2, CH_4) to test for effects of treatment, date, surface water depth, light availability, and the interaction of treatment with the three other terms.

We interpreted significant effects via ANOVA Type III on model coefficients at an alpha value of 0.05 with Satterthwaite approximation for degrees of freedom (*lmertest*). When

categorical coefficients (i.e., treatment, date) were significant, we performed post-hoc pairwise comparisons on model coefficients using difference of least means squares, and interpreted significant differences at alpha value of 0.05. When continuous numeric coefficients (i.e., water depth) were significant, we plotted the parameter to observe the trend. All means are presented as un-transformed means ± 1 SE.

Results

Biomass quantity- Management treatments affected longer-term (> one year after treatment) biomass patterns of a common Great Lakes invasive macrophyte, *Typha x glauca* (Fig. 2). Crushing and harvesting *Typha* eliminated standing litter, while 562.8 ± 111.8 g/m^2 of standing litter remained in un-manipulated *Typha*-dominated controls. Harvesting *Typha* reduced aboveground live biomass relative to stands where *Typha* was crushed or un-manipulated, and this treatment effect ($F_{2, 40} = 7.8$, $p = 0.001$) was independent of a positive effect of water depth ($F_{1, 40} = 28.4$, $p < 0.001$) on aboveground biomass. Longer-term aboveground biomass patterns were similar in 2017 (treatment effect: $F_{2, 63} = 43.8$, $p < 0.001$ and water depth effect: $F_{1, 63} = 6.8$, $p = 0.01$). The reduced biomass is likely due to harvested and crushed stands growing back with shorter *Typha* stems relative to un-manipulated controls in 2016 ($F_{2, 12 =} 16.0$, $p < 0.001$) and 2017 ($F_{2, 12} = 40$, $p < 0.001$), while stem density did not differ among treatments in 2016 ($F_{2, 13} = 3.9$, $p = 0.05$) or 2017 ($F_{2, 13} = 0.3$, $p = 0.8$).

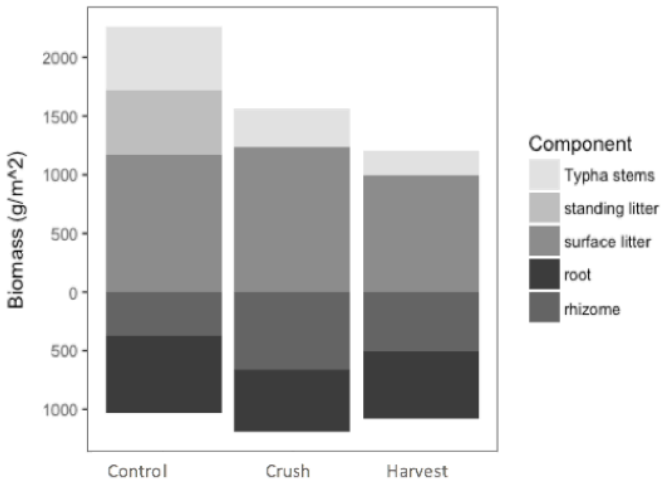


Figure 2. Stacked bar graph of mean biomass by treatment one year after initial treatments were implemented (sampled in early July 2016). Belowground biomass components (i.e., roots and rhizomes) were sampled to approximately 12 cm depth.

Table 2. Aboveground *Typha* metrics by treatment (mean ± SE) sampled one (2016) and two (2017) years after initial treatments were implemented. $^{\vdash}$ indicates data were log-10 transformed for statistical analysis, and within each parameter and year, letters indicate treatment differences.

	Early July 2016			Early July 2017		
	Density (stems/m^2)	**Height (cm)**	**Biomass $^{\vdash}$ (g/m^2)**	**Density (stems/m^2)**	**Height (cm)**	**Biomass $^{\vdash}$ (g/m^2)**
Control	31.1 (2.7)^{a}	205.2 (12.0)^{a}	851.4 (179.6)^{a}	45.1 (6.8)^{a}	224.2 (3.8)^{a}	1075.1 (56.2)^{a}
Crush	38. 2 (3.0)^{a}	158.2 (25.7)^{b}	322.8 (39.8)^{a}	42.9 (3.0)^{a}	168.1 (5.7)^{b}	448.4 (28.7)^{b}
Harvest	41. 3 (2.3)^{a}	130.6 (9.5)^{c}	194.4 (20.4)^{b}	48.7 (3.6)^{a}	136.3 (7.3)^{c}	251. 9 (39.2)^{c}

Unlike for standing litter, crushing and harvesting *Typha* had no longer-term treatment effect ($F_{2, 40} = 1.7$, $p = 0.2$) on surface litter (Table 3). When we examined rhizome and root data separately, we found no treatment effect ($F_{2, 13} = 1.2$, $p = 0.3$) on rhizome density. For root density, treatment had an interactive effect with water depth ($F_{2, 36} = 7.9$, $p = 0.001$), so it was difficult to discern if decreased root density in crush was result of treatment or water depth differences (Appendix I). Neither total belowground biomass (root + rhizome) nor belowground: aboveground biomass ratios differed among management treatments ($p > 0.05$).

Table 3. Treatment means (± SE) of biomass (g/m^2), carbon and nitrogen content for surface litter and belowground pools, one year after initial treatment implementation (sampled July 2016). [b] indicates data were log-10 transformed for statistical analysis, and within each parameter, letters indicate treatment differences (Note: root and rhizome biomass sampled to ~12 cm depth.)

	Surface Litter			Rhizome			Root		
	biomass	**%C**	**%N**	**biomass**	**%C**	**%N**	**biomass** [b]	**%C**	**%N**
Control	1162.1[a] (97.3)	46.5[a] (0.7)	0.50[a] (0.05)	364.9[a] (96.8)	44.5[a] (0.4)	0.47[a] (0.06)	674.7[a] (154.6)	45.6[a] (0.5)	1.32[a] (0.09)
Crush	1230.9[a] (108.0)	47.3[a] (0.6)	0.49[a] (0.06)	668.0[a] (114.9)	44.2[a] (0.4)	0.44[a] (0.03)	524.6[a] (124.7)	46.4[a] (0.2)	1.01[b] (0.09)
Harvest	993.1[a] (97.9)	47.0[a] (0.4)	0.73[a] (0.08)	501.6[a] (117.9)	44.0[a] (0.2)	0.43[a] (0.05)	585.1[a] (197.2)	46.5[a] (0.4)	1.09[a] (0.11)

Biomass carbon- The standing litter comprised ~33% of the total litter biomass in the un-manipulated *Typha* controls (Fig. 2), and constitutes an average standing litter carbon stock of 264.6 ± 52.6 g-C/m^2. Neither harvest nor crush affected other longer-term plant carbon pools, as the %C in surface litter, rhizomes, and roots during the subsequent season was similar across treatments (Table 3; $p > 0.05$). C:N ratios of *Typha* biomass components were largely unaffected by treatment, with the exception of a treatment effect on roots ($F_{2, 37} = 3.6$, $p = 0.04$), which had higher C:N ratios in the crushed stands (50.4 ± 3.5) compared to C:N ratios in the control stands (37.4 ± 3.5). This difference is likely driven by lower %N in the crush stand roots (Table 3; treatment effect: $F_{2, 37} = 4.6$, $p = 0.02$).

Aqueous carbon- Experimental treatments did not affect surface water POC (Table 4; treatment effect: $F_{2, 23} = 2.8$, $p = 0.07$), which decreased from July to August 2016 across the marsh (date effect: $F_{1, 23} = 6.0$, $p = 0.02$). Significant interactive effects between treatment and date indicated distinct longer-term and immediate responses to treatments for surface water DOC ($F_{2, 15} = 4.5$, $p = 0.03$), and for pore water DOC ($F_{2, 16} = 8.4$, $p = 0.003$), POC ($F_{2, 17} = 4.3$, $p = 0.03$), and acetate ($F_{2, 25} = 4.7$, $p = 0.02$). Further, treatment and water depth had an interactive effect on surface water DOC ($F_{2, 14} = 4.3$, $p < 0.001$), and on pore water DOC ($F_{2, 20} = 4.3$, $p = 0.006$) and

acetate ($F_{2, 25} = 4.7$, $p = 0.02$), indicating treatments had distinct relationships between water depth and these water C concentrations (Appendix II).

Surface water DOC was greater in harvested stands than in crushed stands, but neither treatment differed from control stands one year after initial treatment (Table 4). Crushed stands had more pore water acetate relative to control and harvested stands in longer-term. There was an immediate decrease in pore water acetate from July to August in control and crushed stands, but not in harvested stands, suggesting harvesting interfered with a seasonal reduction of acetate. Crushing caused an immediate pulse of surface water DOC and pore water POC that did not occur in control or harvested stands. In contrast, pore water DOC increased from July to August in control and harvested stands, but did not change in crushed stands. The divergent trend between immediate responses of pore water C substrates (i.e., increased POC and decreased DOC in crushed stands relative to control stands) suggests crushing may alter rates of C decomposition.

Table 4. Particulate- and Dissolved- Organic Carbon (DOC, POC) and acetate treatment means (± SE) of surface and pore (10-cm below water surface) water. July indicates longer-term response from previous year's treatment, and August indicates immediate response from present year's treatment. ⊦ indicate data were log-10 transformed for statistical analysis, and within each parameter, letters indicate treatment differences (Note: July 2017 DOC analyzed on different TOC analyzer than 2016 DOC).

Surface Water	**POC** ⊦		**DOC*** ⊦		**DOC** ⊦
	JUL 2016	AUG 2016	JUL 2016	AUG 2016	JUL 2017
Control	505.72[a] (48.54)	282.34[b] (209.56)	17.03[ab] (9.44)	20.34[ab] (12.45)	10.12[a] (3.20)
Crush	467.29[a] (96.29)	677.06[b] (281.05)	17.08[a] (2.65)	24.49[c] (5.47)	6.86[a] (1.08)
Harvest	1198.73[a] (560.19)	1184.65[b] (583.58)	31.85[b] (10.27)	33.75[bc] (12.48)	7.09[a] (2.4)
Pore Water	**POC** ⊦		**DOC*** ⊦		**Acetate*** ⊦
	JUL 2016	AUG 2016	JUL 2016	AUG 2016	JUL 2016	AUG 2016
Control	97.97[a] (20.94)	92.99[a] (25.88)	16.77[a] (2.58)	21.28[b] (4.47)	2.27[a] (0.87)	0.02[c] (0.01)
Crush	118.13[a] (21.45)	429.13[b] (113.22)	15.99[a] (1.80)	21.39[a] (3.31)	2.54[b] (0.62)	0.20[c] (0.13)
Harvest	157.62[ac] (8.99)	404.22[bc] (179.60)	17.32[a] (3.49)	26.19[b] (7.97)	1.02[ac] (0.66)	0.11[c] (0.11)

Abiotic consequences- A significant interactive effect between treatment and date ($F_{2, 49}$= 32.7, $p < 0.001$) indicated distinct longer-term and immediate responses to treatments for light transmission (Table 5). In the longer-term, a greater percent of light reached the water surface in the crush and harvest stands than in control stands, while immediately following treatment, light to the water surface decreased in crushed stands, and increased in harvested stands. There was an interactive effect of treatment and date ($F_{2, 42}$= 13.0, $p < 0.001$) on water temperature; temperature increased from July to August in crushed plots, but not in control or harvested plots (Table 5).

Table 5. Abiotic variables from gas flux plots during 2017 July and August sampling campaigns. Water depth and PAR above-canopy were used as covariates in C flux statistical analyses, and are presented here for reference. We directly tested for treatment effects on % light transmitted to water surface and on water temperature, and letters indicate treatment differences.

	Water Depth (cm)		**PAR above-canopy (umol/s/m^2)**		**Light transmitted (%)**		**Water temperature (°C)**	
	JUL	AUG	JUL	AUG	JUL	AUG	JUL	AUG
Control	35.50 (5.01)	22.25 (2.81)	1236.25 (149.27)	856.25 (272.28)	10.11^{a} (3.53)	3.49^{c} (1.05)	21.88^{a} (1.17)	22.88^{a} (1.30)
Crush	20.75 (1.05)	21.89 (1.15)	1172.08 (127.08)	1107.78 (197.71)	24.75^{b} (2.28)	13.77^{c} (2.94)	20.41^{a} (0.31)	23.28^{b} (0.79)
Harvest	26.83 (1.69)	31.44 (2.91)	1354.64 (136.54)	939.11 (187.80)	21.42^{b} (3.66)	64.02^{d} (6.67)	21.75^{a} (0.58)	22.61^{a} (0.42)

C Flux- CO_2 uptake had distinct longer-term and immediate responses to management treatments (Fig 3; treatment x date effect: $F_{2, 45}$ = 17.1, $p < 0.001$). Over longer-term, there was increased CO_2 uptake in harvested stands relative to controls. Immediately after treatment, crushing and harvesting *Typha* reduced CO_2 uptake, and on average, these stands were sources of CO_2, emitting 97.7 ± 15.5 umol/m^2/min and 56.1 ± 52.4 umol/m^2/min respectively. The effects of treatment and sampling date on CH_4 emissions were significant and independent of each other (treatment x date effect: $F_{2, 30}$ = 1.1, $p = 0.35$, treatment effect: $F_{2, 30}$ = 5.8, $p = 0.007$,

date effect: $F_{1, 30} = 14.3$, $p < 0.001$). Harvested stands had higher CH_4 emissions than control stands in both July and August. Across the marsh, CH_4 emissions increased from July to August (Fig 3).

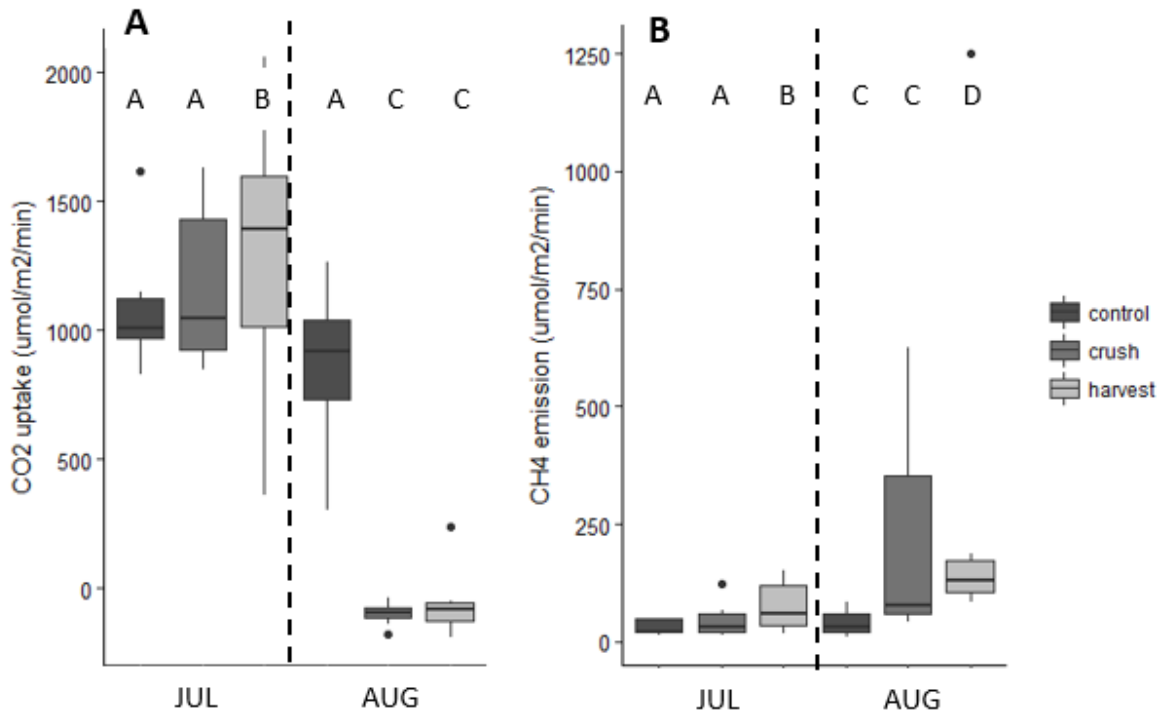


Figure 3. Boxplots of *in-situ* A) Carbon dioxide (CO_2) uptake and B) Methane (CH_4) emission for July and August 2017. Dotted lines indicate 2017 treatment implementation. Methane data were log-10 transformed for statistical analysis, and within each parameter, letters indicate treatment and/or date differences.

We converted and scaled the mean gas values to estimate how treatments affect the radiative forcing of the wetland (Appendix III). Longer-term responses suggest that all stands were still net sinks of CO_2 equivalents, but harvesting reduced CO_2 equivalent uptake by approximately 30% relative to controls. The immediate radiative forcing effects are also noteworthy; while control stands were took up ~27 g-CO_2 equivalents/m^2/day, harvested stands were a net source of approximately ~208 g-CO_2 equivalents/m^2/day.

Over longer-term, CO_2 uptake was positively correlated with aboveground biomass across the marsh (biomass effect: $F_{1, 13} = 50.1$, $p < 0.001$) and the relationship differed by treatment (treatment x biomass effect: $F_{2,11} = 16.6$, $p < 0.001$), suggesting more CO_2 uptake per unit biomass in harvested stand than in control stands (Fig. 4A). CH_4 flux rates did not vary with changes in biomass ($F_{1, 16} = 1.8$, $p = 0.20$), but there was a linear trend between CH_4 emissions and CO_2 uptake (Fig. 4B; $F_1 = 6.5$, $p = 0.02$) that was independent of treatment.

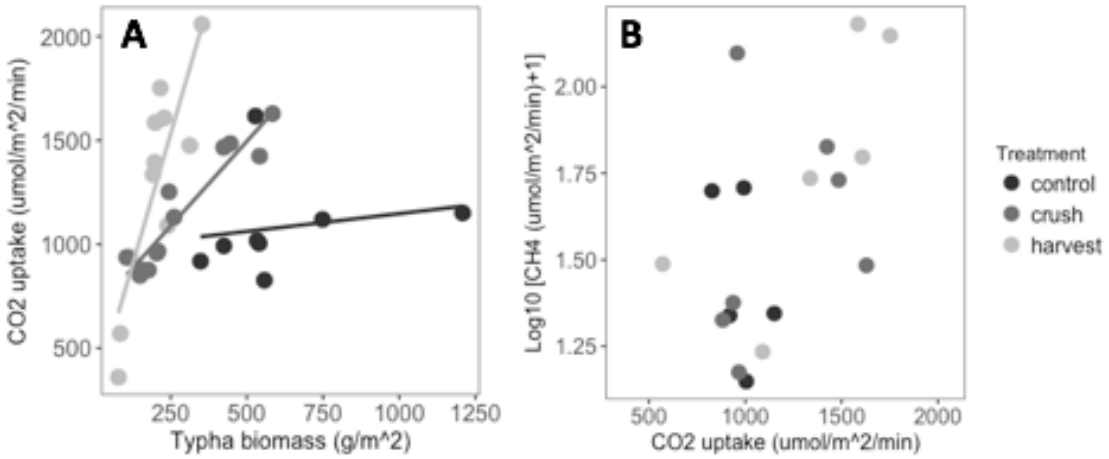


Figure 4. A) Carbon dioxide (CO_2) uptake vs. *Typha* aboveground biomass B) Methane (CH_4) emissions vs. CO_2 uptake. Each point represents a July 2017 measurement, and points are colored by treatment. Linear mixed effects regression indicated an interactive effect of treatment and *Typha* biomass on CO_2 uptake (linear trend lines colored by treatment), but there the relationship between of CH_4 emissions and CO_2 uptake was independent of treatment.

Discussion

Our study addresses critical gaps in knowledge of ecosystem responses to invasive plant management (Petersen et al. 2003, Vaughn 2010, Wagner et al. 2008) and furthers our collective understanding of freshwater carbon cycling (Mitsch et al. 2013, Bridgham et al. 2006). We examined how large-scale (60 m x 60 m) harvested and crushed stands compared to un-manipulated *Typha*-dominated control stands. Regarding longer-term (> 1 year) effects, we

found treatments reduced standing litter and aboveground biomass, along with increased rates of CO_2 uptake and CH_4 emission in harvested stands. We also quantified within season comparisons of treated stands (before/after treatment) to highlight immediate (< 1 month) effects; we observed pulses of surface water DOC and alterations of pore water C in crushed stands, along with immediate CO_2 release in treated stands, and elevated CH_4 with harvest.

Long-term effects (inter-seasonal consequences)

One year after treatment, *Typha* grew back shorter in mechanically treated stands relative to un-manipulated controls, likely because the plants were disturbed during the peak of the growing season and thus carbohydrates and nutrients in growing stem tissues were lost (Hall & Zedler 2010). However, stem density was similar across treatments, evidence of the rhizome storage capacity and persistence of clonal *Typha* (Elgersma et al. 2015, Asaeda et al. 2008). *Typha* persistence and continued dominance one year after treatment may also explain why root biomass was the same across treatments.

While repeated treatment over multiple seasons may be necessary for mechanical management techniques to effectively draw down belowground *Typha* resources, the aboveground structural effects one year after treatment are notable. Harvesting and crushing *Typha* biomass eliminated standing dead stems, a well-known feedback that reinforces invasive plant dominance (Farrer & Goldberg 2009, Vaccaro et al. 2009, Holdredge & Bertness 2010). Treatments also increased light transmission to the water surface, which may stimulate native seed banks if surface water depth permits germination (Lishawa et al. 2015). Thus, both mechanical techniques had similar effects on aboveground structure, offering potential support for plant diversity and wildlife habitat.

It is important to consider how the fates of standing *Typha* litter in harvest and crush techniques could have different consequences on decomposition and other soil respiration processes that support carbon-based wetland function. Standing litter in un-manipulated stands had 264.5 ± 53.6 g-C/m^2 and 1.6 ± 0.3 g-N/m^2, substantial pools of organic matter that will likely become labile surface litter in subsequent growing seasons; removing this litter via harvesting may decrease C and N inputs to the soil pore water, while crushing it may increase C and N inputs to the soil pore water. Litter quantity and quality can have biochemical effects on decomposition rates (Elgersma et al. 2012, Grasset et al. 2017), but neither surface litter density nor litter C:N content differed across our treatments. While pore water DOC and POC were similar across treatments over the longer-term, increased acetate in the crushed stands suggests differences in soil water processes, potentially due to the anaerobic decomposition of increased plant material on the soil surface (Laanbroek 2010, Megonigal et al. 2004). Investigating carbon storage in rhizomes via cellulose analysis, and measuring additional specific water-borne substrates via spectral analysis may reveal clearer patterns of how management techniques affect longer-term plant-mediated C pools (Asaeda et al. 2008, Inglett et al. 2012, Rothman & Bouchard 2007).

While harvesting decreased aboveground *Typha* stem biomass one year after treatment, harvested stands took up more CO_2 relative to control stands. This uptake is a net value (i.e., net ecosystem exchange) that depends on CO_2 uptake by primary producers (plants + algae) and CO_2 release via autotrophic and heterotrophic respiration. The pattern of increased CO_2 uptake by harvested stands could be due to the increased light transmittance to water surface we observed, which may increase primary production in the water column (i.e. phytoplankton; Yoshiyama et al. 2009). Harvesting invasive *Typha* increased CH_4 emissions relative to controls

one year after treatment, but CH_4 emissions were not significantly related to aboveground biomass, contrary to other findings (Lawrence et al. 2017, Sutton-Grier & Megonigal 2010). Still, the relationship between CH_4 emissions and CO_2 uptake suggests that CH_4 production increases as primary production increases. We quantified linear diffusion trends of CH_4 from approximately half of our total sampling points, and addressing the nuances (i.e. ebullition versus diffusion, soil emissions versus plant transport) associated with CH_4 emissions would help us more fully understand the carbon balance response to management (Laanbroek 2010, Rietl et al. 2017, Rothman & Bouchard 2007).

Immediate effects (intra-seasonal effects)

Less than one month after harvesting and crushing, we quantified an immediate reduction in biomass, paired with an immediate reduction in CO_2 uptake. Light transmission patterns reflected what structurally happened to the biomass; harvesting *Typha* increased light penetration to the water surface, and crushing *Typha* decreased light to water surface. We found immediate increases in DOC in pore water of harvested stands, where plants were growing back, and likely exuding fresh C as they respired (Dijkstra et al. 2013). On the other hand, we found increased POC in pore water of crushed stands, where breakdown of macro-organic matter probably occurred at a slower rate because stem conduits bringing oxygen to rhizosphere were trampled (Ehrenfeld et al. 2005).

Surface water DOC increased where *Typha* was crushed into the surface. This pulse of carbon (substrate for microbes) paired with decreased light penetration (limit on primary production) might explain the immediate increase in CH_4 emissions in crushed stands (Morrissey et al. 2014, Inglett et al. 2012). Further, nutrients leaching from fresh *Typha* may have stimulated microbial processes to increase C emissions (Rietl et al. 2017, Grasset et al. 2017). Thus, the

two treatments likely had different mechanisms of CH_4 emissions; the greenhouse gas diffusing through cut stems in harvested stands (Laanbroek 2010, Dingemans et al. 2011), and anaerobic decomposition releasing methane from surface water in crushed stands (Megonigal et al. 2004).

Management implications

Our results suggest that the longer-term structural effects of harvesting may support management objectives of improving habitat and plant diversity, without decreasing primary production capacity of the wetland ecosystem. On the other hand, increased CH_4 emissions from harvested relative to control stands constitute an ecosystem disservice in response to management. CO_2 equivalent uptake was approximately 30% less in harvested stands relative to controls, suggesting the increased CH_4 emissions impacted the wetland's ability to mitigate sources of radiative forcing from the surrounding landscape over the longer-term.

Crushing biomass had immediate biochemical effects (i.e. increased DOC in surface water, and decreased POC in porewater) that may potentially affect internal carbon cycling. These chemical effects should be taken into account and monitored. In addition to carbon sequestration consequences, shifts in carbon can have trophic implications at multiple scales, so investigating these carbon pools along with waterfowl, macroinvertebrate, and microbial communities could help evaluate wetland functional diversity response to management. Ultimately, scientists and land managers should continue to apply understanding of wetland carbon dynamics to assessment of wetland management efforts.

References

Asaeda, T, Sharma, P, Rajapakse, L (2008) Seasonal patterns of carbohydrate translocation and synthesis of structural carbon components in *Typha angustifolia*. *Hydrobiologia* 607 (1): 87-101

Bennett, E, Peterson, G, & Gordon, L (2009) Understanding relationships among multiple ecosystem services. *Ecology Letters* 12 (12): 1394-1404

Beule, JD (1979) Control and management of cattails in southeastern Wisconsin wetlands. *Technical Bulletin No. 112, Department of Natural Resources, Madison, WI*

Berke, K (2017) Nutrient removal and vegetation recovery through successive harvesting of the invasive hybrid cattail (*Typha* × *glauca*) in Great Lakes coastal wetlands *ProQuest Dissertations & Theses Global* (Order No. 10636445)

Bodelier, PLE & Laanbroek, HJ (2004) Nitrogen as a regulatory factor of methane oxidation in soils and sediments. *FEMS Microbiology Ecology* 47 (3): 265-277

Bridgham, SD, Megonigal, JP, Keller, JK, Bliss, NB, & Trettin, C (2006) The carbon balance of North American wetlands. *Wetlands* 26 (4): 889-916

Carmichael, MJ, Bernhardt, ES, Braeur, SL, and Smith, WK (2014) The role of vegetation in methane flux to the atmosphere: should vegetation be included as a distinct category in the global methane budget? *Biogeochemistry* 119: 1-24

Carson, BD, Lishawa, SC, Tuchman, NC, Monks, AM, Lawrence, BA & Albert, DA (2018) Harvesting invasive plants to reduce nutrient loads and produce bioenergy: an assessment of Great Lakes coastal wetlands. *Ecosphere*, 9 (6): Article e02320

Dijkstra, FA, Carrillo, Y, Pendall, E, & Morgan, JA (2013) Rhizosphere priming: A nutrient perspective. *Frontiers in Microbiology* 4: 1-8

Dingemans, BJ, Bakker, ES & Bodelier, PL (2011) Aquatic herbivores facilitate the emission of methane from wetlands. *Ecology* 92 (5): 1166-1173

Ehrenfeld, JG, Ravit, B, & Elgersma, K (2005) Feedback in the plant-soil system. *Annual Review of Environment and Resources* 30: 75-115

Elgersma, KJ, Wildova, R, Martina, JP, Currie, WS, & Goldberg, DE (2015) Does clonal resource translocation relate to invasiveness of *Typha* taxa? Results from a common garden experiment. *Aquatic Botany* 126: 48-53

Elgersma, KJ, Yu, S Vor, T & Ehrenfeld, JG (2012) Microbial-mediated feedbacks of leaf litter on invasive plant growth and interspecific competition. *Plant and Soil* 356: 341-355

Farrer, EC & Goldberg, DE (2009) Litter drives ecosystem and plant community changes in cattail invasion. *Ecological Applications* 19 (2): 398-412

Fogli, S, Brancaleoni, L, Lambertini, C, & Gerdol, R (2014). Mowing regime has different effects on reed stands in relation to habitat. *Journal of Environmental Management* 134: 56-62

Galatowitsch, SM, Anderson, NO, & Ascher, PD (1999) Invasiveness in wetland plants in temperate North America. *Wetlands* 19 (4): 733-755

Grasset, C, Levrey, LH, Delolme, C, Arthaud, F, & Bornette, G (2017) The interaction between wetland nutrient content and plant quality controls aquatic plant decomposition. *Wetlands Ecology and Management* 25 (2): 211-219

Grosse, W, Armstrong, J, & Armstrong, W (1996) A history of pressurized gas-flow studies in plants. *Aquatic Botany* 54: 87-100

Hall, S & Zedler, J (2010) Constraints on Sedge Meadow Self-Restoration in Urban Wetlands. *Restoration Ecology*, 18 (5): 671-680

Holdredge, C & Bertness, MD (2010) Litter legacy increase the competitive advantage of invasive *Phragmites australis* in New England wetlands. *Biological Invasions* 13: 423-433

Holland, EA, Robertson, GP, Greenburg, J, Froffman, PM, Boone, RD, & Gosz, JR (1999) Soil CO_2, N_2O, CH_4 Exchange, in *Standard Soil Methods for Long-Term Ecological Research*. Oxford University Press, New York, New York. Robertson, GP, Coleman, DC, Bledsoe, CS, Sollins, P (Eds.): 185-201

Inglett, KS, Inglett, PW, Reddy, KR, & Osborne, TZ (2012) Temperature sensitivity of greenhouse gas production in wetland soils of different vegetation. *Biogeochemistry* 108: 77-90

Jakubowski, AR, Casler, M. & Jackson, RD (2010) The benefits of harvesting wetland invaders for cellulosic biofuel: an ecosystem services perspective. *Restoration Ecology* 18: 789-795

Kandel, T, Elsgaard, L, Karki, S, & Laerke, P (2013) Biomass yield and greenhouse gas emissions from a drained fen peatland cultivated with reed canary grass under different harvest and fertilizer regimes. *BioEnergy Research* 6: 883-895

Kayranli, B, Scholz, M, Mustafa, A, & Hedmark, A (2010) Carbon storage and fluxes within freshwater wetlands: a critical review. *Wetlands* 30: 111-124

Keyport, S, Carson, BD, Johnson, O, Lawrence, BA, Lishawa, SC ,Tuchman, NC, & Kelly, JJ (2018) Effects of experimental harvesting of an invasive hybrid cattail on wetland structure and function. *Restoration Ecology*, accepted July 7, 2018

Kotowski, W, Jablonska, E, & Bartoszuk, H (2013) Conservation management in fens: Do large tracked mowers impact functional plant diversity? *Biological Conservation* 167: 292-297

Laanbroek, HL (2010) Methane emission from natural wetlands: interplay between emergent macrophytes and soil microbial processes: A mini-review. *Annals of Botany* 105: 141-153

Larkin, DJ, Monika, FJ, Lishawa, SC, Geddes, P, & Tuchman, NC (2012) Mechanism of dominance by the invasive hybrid cattail *Typha x glauca*. *Biological Invasions* 14: 65-77

Lawrence, BA, Lishawa, SC, Hurst, N, Castillo, BT, & Tuchman, NC (2017) Wetland invasion by *Typha x glauca* increases soil methane emissions. *Aquatic Botany* 137: 80-87

Lishawa, SC, Lawrence, BA, Albert, DA, & Tuchman, NC (2015) Biomass harvest of invasive *Typha* promotes diversity in Great Lakes coastal wetland. *Restoration Ecology* 23 (3): 228-237

Martin, JL & Blossey, B (2013) The Runaway Weed: Costs and failures of *Phragmites australis* management in the USA. *Estuaries and Coasts* 36: 626-632

Megonigal, JP, Hines, ME & Visscher, PT (2004) *Anaerobic Metabolism: Linkages to Trace Gases and Aerobic Processes*, in *Biogeochemistry*. Elsevier-Pergamon, Oxford, UK. Schlesinger, WH (Ed.): 317-424

Mitsch, WJ, Bernal, B, Nahlik, AM, Mander, U, Zhang, L, Anderson, CJ, Jorgensen, SE, & Brix, H (2013) Wetlands, carbon, and climate change. *Landscape Ecology* 28: 583-597

Morrissey EM, Berrier DJ, Neubauer, SC, & Franklin, RB (2014) Using microbial communities and extracellular enzymes to link soil organic matter characteristics to greenhouse gas production in a tidal freshwater wetland. *Biogeochemistry* 117: 473-490

Myhre, G, Shindell, D, Bréon, FM Collins, W, Fuglestvedt, J, Huang, J, Koch, D J.-F. Lamarque, JF, Lee, D, Mendoza, B, Nakajima, T, Robock, A, Stephens, G, Takemura, T & Zhang, H (2013) Anthropogenic and Natural Radiative Forcing. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Osland, MJ, Gonzalez, E, & Richardson, CJ (2011) Restoring diversity after cattail expansion: disturbance, resilience, and seasonality in a tropical dry wetland. *Ecological Applications* 21 (3): 715-728

Peralta, AL, Muscarella, ME, & Matthews, JW (2018) Wetland management strategies lead to tradeoffs in ecological structure and function. *Elementa Science of the Anthropocene* 5: article 74

Petersen, JE, Kemp, WM, Bartleson, R, Boynton, WR, Chen, C, Cornwell, JC, Gardner, RH, Hinkle, DC, Houde, ED, Malone, TC, Mowitt, WP, Murray, L, Sanford, LP, Stevenson,

JC, Sundberg, KL, & Suttles, SE (2003) Multiscale Experiments in Coastal Ecology: Improving Realism and Advancing Theory. *BioScience* 53 (12): 1181-1197

Quirion B, Simek Z, Dávalos A, & Blossey B (2018) Management of invasive *Phragmites australis* in the Adirondacks: a cautionary tale about prospects of eradication. *Biological Invasions* 20: 59-73

R version 3.4.1 (2017-06-30) -- "Single Candle", Copyright (C) 2017 The R Foundation for Statistical Computing, Platform: x86_64-w64-mingw32/x64 (64-bit)

Rietl, AJ, Nyman, JA, Lindau, CW, & Jackson, CR (2017) Wetland methane emissions altered by vegetation disturbance: An interaction between stem clipping and nutrient enrichment. *Aquatic Botany* 136: 205-211

Rodríguez, JP, Beard Jr, TD, Bennett, EM, Cumming, GS, Cork, SJ, Agard, J, Dobson, AP & Peterson, GD (2006) Trade-offs across space, time, and ecosystem services. *Ecology and society* 11 (1): article 28

Rothman, E & Bouchard, V (2007) Regulation of carbon processes by macrophyte species in a Great Lakes coastal wetland. *Wetlands* 27 (4): 1134-1143

Sierszen, ME, Morrice, JA, Trebitz, AS, & Hoffman, JC (2012) A review of selected ecosystem services provided by coastal wetlands of the Laurentian Great Lakes. *Aquatic Ecosystem Health & Management* 15 (1): 92–106

Suding, KN, Gross, KL, & Houseman, GR (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution* 19 (1): 46-53

Sutton-Grier, AE & Megonigal, JP (2010) Plant species traits regulate methane production in freshwater wetland soils. *Soil Biology & Biochemistry* 43: 413-420

Tuchman, NC, Larkin, DJ, Geddes, P, Wildova, R, Jankowski, K, & Goldberg, DE (2009). Patterns of environmental change associated with *Typha x glauca* invasion in a Great Lakes coastal wetland. *Wetlands* 29 (3): 964-975

Uzarski, DG, Brady, VJ, Cooper, MJ, Wilcox, DA, Albert, DA, Axler, RP, Bostwick, P, Brown, TN, Ciborowski, JJH, Danz, NP, Gathman, JP, Gehring, TM, Grabas, GP, Garwood, A Howe, RW, Johnson, LB, Lamberti, GA, Moerke, AH, Murry, BA, Niemi, GJ, Norment, CJ, Ruetz, CR, Steinman, AD, Tozer, DC, Wheeler, R, O'Donnell, TK, & Schneider, JP (2017) Standardized measures of coastal wetland condition: implementation at a Laurentian Great Lakes basin-wide scale. *Wetlands* 37 (1):15-32.

Vaccaro, LE, Bedford BL, & Johnston CA (2009) Litter accumulation promotes dominance of invasive species of cattails (*Typha* Spp.) in Lake Ontario Wetlands. *Wetlands* 29 (3): 1036-1048

Vaughn, C (2010) Biodiversity losses and ecosystem function in freshwaters: Emerging conclusions and research directions. *BioScience* 60 (1): 25-35

Wagner, KI, Gallagher, SK, Hayes, M, Lawrence, BA, & Zedler, JB (2008) Wetland restoration in the new millennium: do research efforts match opportunities? *Restoration Ecology* 16 (3): 367-372

Winton, SR & Richardson, CJ (2017) Top-down control of methane emission and nitrogen cycling by waterfowl. *Ecology* 98 (1): 265-277

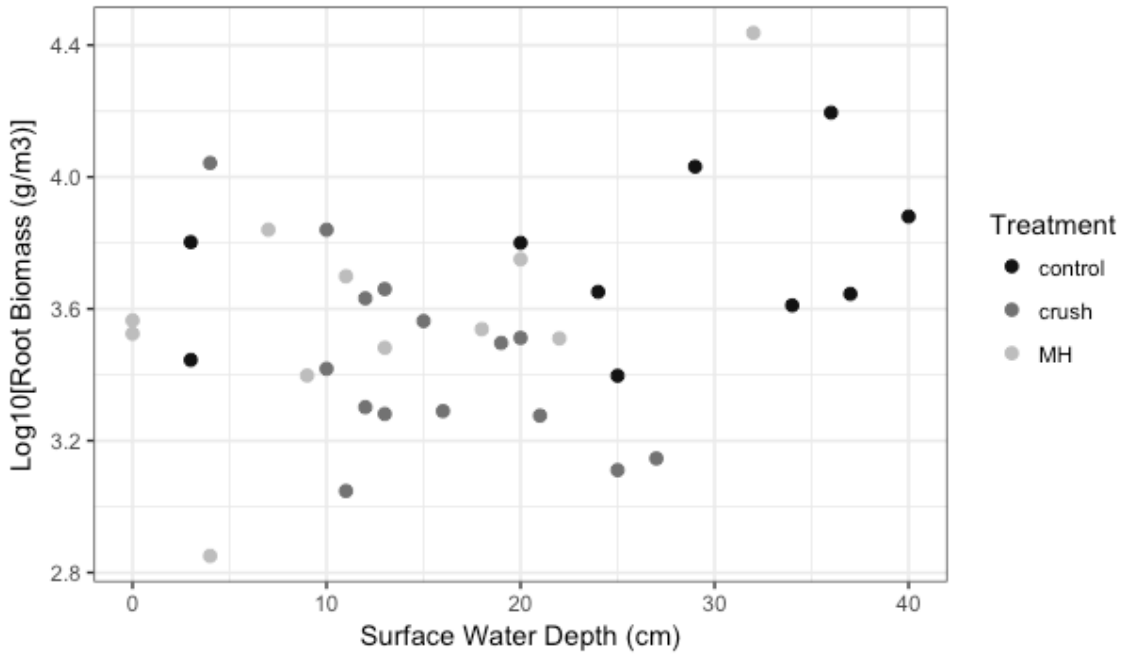
Yoshiyama, K Mellard, JP Litchman, & E Klausmeier, CA (2009) Phytoplankton Competition for Nutrients and Light in a Stratified Water Column. *The American Naturalist* 174 (2): 190-203

Zedler, JB (2009) Feedbacks that might sustain natural, invaded and restored states in herbaceous wetlands, in *New models for ecosystem dynamics and restoration*. Island Press, Washington, D.C. Hobbs R., K. Suding (Eds.): 236-258

Zedler, JB & Kercher S (2005) Wetland resources: status, trends, ecosystem services, and restorability. *Annual Review of Environment and Resources* 30: 39-74

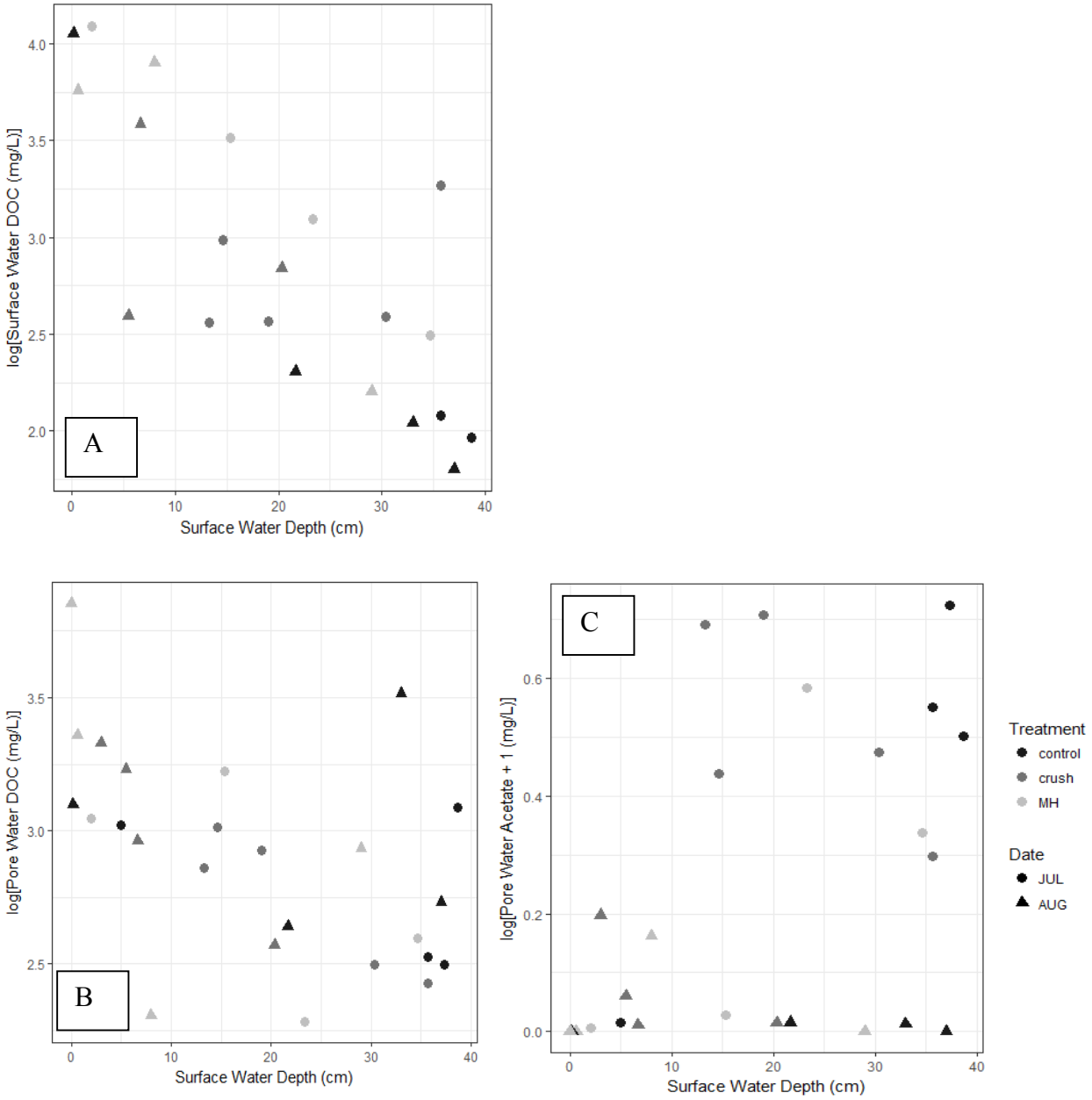
Appendices

Appendix I.



Root biomass vs. surface water depth. Each point represents a July 2016 measurement, and points are colored by treatment. Linear mixed effects regression indicated an interactive effect of treatment and surface water depth on root biomass.

Appendix II.



A) Surface water DOC, B) pore water DOC, and C) pore water acetate vs. surface water depth. Each point represents a plot measurement. Colors represent treatment, shapes represent date; JUL= Pre 2016 treatment, AUG= Post 2016 treatment. Linear mixed effects regression indicated an interactive effect of treatment and surface water depth on these aqueous C concentrations.

Appendix III.

Radiative forcing (in CO_2 equivalents) was estimated by converting flux rates (umol/m^2/min) to weights of C gas using their molar masses, then multiplying the CH_4 data by 28. We scaled the net forcing to radiative forcing per area per day, and to radiative forcing per day across the area of our study site. (Note: sample size for methane data was smaller than sample size for CO_2 data)

		n		Average Flux (umol/m^2/min)		CO2 equivalents (g-CO2/m2/min)			Daily net forcing	
Treatment	**Date**	**CO2**	**CH4**	**CO2**	**CH4**	**CO2**	**CH4**	**Net forcing**	**g-CO2/m2/day**	**g-CO2/day across 5.4 ha**
Control	Jul	8	5	1080.95	30.82	-0.05	0.01	-0.03	-48.56	-2,622,226.92
Crush	Jul	12	7	1154.78	47.02	-0.05	0.02	-0.03	-42.75	-2,308,765.26
Harvest	Jul	11	6	1288.22	75.18	-0.06	0.03	-0.02	-33.00	-1,782,015.01
Control	Aug	4	3	853.46	42.13	-0.04	0.02	-0.02	-26.83	-1,448,692.15
Crush	Aug	8	3	-97.65	247.99	0.00	0.11	0.12	166.57	8,994,829.41
Harvest	Aug	7	6	-56.12	312.82	0.00	0.14	0.14	205.86	11,116,679.24

How do invasive *Typha* management treatments alter plant-soil feedbacks in northern Great Lakes coastal wetlands?

Introduction

Plant–soil interactions are important to wetland capacities to store carbon and filter nutrients (Ehrenfeld et al. 2005), functions that are increasingly relevant in the era of anthropogenic climate change and eutrophic waters. Flooded soils promote carbon accumulation in organic soils by enabling high rates of primary productivity, and slowing rates of organic matter decomposition (i.e., oxygen is quickly consumed, requiring microbes to use other substrates to respire). Simultaneously, dissimilatory respiration pathways can produce greenhouse gases (carbon dioxide, methane, nitrous oxide), but also assimilate and mineralize nutrients, cycling and slowing excess nutrients from runoff. Understanding the ecological mechanisms responsible for these ecosystems services is necessary in the context of landscape stressors and management efforts (Peralta et al. 2018, Petersen et al. 2003).

Because wetlands occur at the boundaries of terrestrial and aquatic environments, and are often sinks for the surrounding landscape, these systems are susceptible to multiple stressors (i.e., nutrient-rich runoff, flashy hydroperiods, invasive propagules) that promote the dominance of invasive plants (Zedler & Kercher 2005). Non-native plant species, specifically clonal graminoids, are a prevalent management concern because their dense monocultures reduce plant diversity, reduce wildlife habitat quality, and alter carbon and nutrient cycling (Galatowitsch et al. 1999, Zedler & Kercher 2005, Frieswyk & Zedler 2007, Ehrenfeld 2010). While treating plants with herbicide is a common technique used in the United States to control wetland invasive plants (Martin & Blossey 2013), there is a resurgence of interest in using non-chemical control methods. Harvesting (i.e., mowing and removing) invasive biomass can increase plant

diversity, remove nutrient-dense plant tissues, and provide a potential source of biofuel (Lishawa et al. 2015, Jakubowski et al. 2010, Carson et al. 2018). Creating aquatic connectivity channels (i.e., cutting and drowning cut stems, and removing aboveground biomass) can promote open water patches, which improve habitat heterogeneity and support larval fish movement (Schummer et al. 2012). While these management techniques typically focus on aboveground structural attributes, there is little known on how these techniques affect the belowground dynamics (i.e., root growth, organic matter decomposition) that are critical to carbon and nutrient cycling.

Plants require macronutrients (i.e., nitrogen, potassium, calcium, magnesium, phosphorus, and sulfur) in large concentrations, and require smaller amounts of micronutrients such as iron and manganese (Barak 1999). Wetland plant adaptations for surviving in flooded soils include aeration of soil by roots, which also exude specific enzymes for microbial nutrient cycling (Grosse et al. 1996, Ehrenfeld et al. 2005). Further, root exudates can facilitate uptake of certain nutrients (i.e., make compounds more mobile), and reduce toxic levels of other nutrients (i.e., make compounds less soluble; Paterson 2003). Many of the simple sugars exuded by roots are simply excess carbon that can be broken down via decomposition (Paterson 2003), and the microbial activity consuming these exudates is a key process of plant-soil interactions.

To assess how wetland restoration affects ecosystem functioning, it is necessary to understand how management techniques alter the interactions between wetland root properties, nutrient availability rates, and microbial processes in the rhizosphere. Mechanical treatment of invasive plants can shift belowground biomass, and in turn affect the dominant microbial processes that contribute to the carbon and nutrient functions of wetlands (i.e., methanogenesis, methane-oxidation, nitrification, denitrification, reduction-oxidation reactions). Root biomass

may be a proxy for carbon exudates and oxygen availability (Welsch & Yavitt 2007, Grosse et al. 1996), and may be indicative of biogeochemical responses to invasive plant management. Because invasive macrophytes often re-grow from cut stems and existing rhizomes, harvesting may stimulate root growth and accelerate microbial processes (i.e., rhizosphere priming; Dijkstra et al. 2013). Conversely, creating aquatic channels cuts off the conduit between the atmosphere and rhizosphere by flooding cut macrophyte stems, so this management technique might inhibit root growth, reduce carbon exudates, and limit rhizosphere oxygenation. To answer ecological questions about how mechanical disturbance to invaded stands affects soil properties and processes, we leveraged a large-scale wetland management experiment conducted in *Typha*-dominated wetlands in the northern Laurentian Great Lakes (USA). Specifically, we hypothesized:

1) Relative to un-manipulated *Typha*-dominated controls, channel creation would reduce invasive macrophyte aboveground and belowground biomass, and result in decreased soil respiration rates.
2) Relative to un-manipulated *Typha*-dominated controls, harvested stands would have more root biomass, and result in increased soil respirations rates.
3) Channel creation would increase plant available nutrients relative to un-manipulated *Typha*-dominated controls due to reduced plant nutrient demand, but harvesting would not affect plant available nutrients due to active regrowth of plants.

Methods

Our study took place in two northern Laurentian Great Lakes coastal wetland complexes classified as palustrine systems with emergent vegetation (Cowardin 1979), all currently dominated by invasive *Typha*. Cheboygan marsh is on the northern shores of Lake Huron near

the city of Cheboygan, Michigan (USA) and St. Ignace marsh is situated just west of the Straights of Mackinaw in northern Lake Michigan, west of St. Ignace, Michigan (Fig. 1A).

Experimental design- In July 2016, we implemented a complete randomized block design, with two blocks of treatments at St. Ignace (hereafter St. Ignace East and St. Ignace West), and one block at Cheboygan (Fig. 1A). Four treatment plots (32 m x 64 m each) were randomly assigned within each block, with all treatments present in each block (Fig. 1B): *Typha*-dominated control (Control), aboveground biomass cut and removal (Harvest), *Typha*-dominated control with an open-water aquatic channel (8 m x 48 m in middle of plot; Control + Channel), and harvested matrix with an open-water aquatic channel (Harvest + Channel). To harvest, we mowed and removed biomass 20 cm above the water surface with a Softrak harvester (Loglogic, England), an amphibious tracked vehicle designed to cut and remove vegetation above water with low ground pressure in wetland environments. To create aquatic channels, we cut vegetation below the water at the soil surface using Aquatic Vegetation Groomers (Weeders Digest, USA), aquatic weedwackers with two circular reciprocating blades, and we completely removed all cut aboveground biomass and surface litter from the channels by hand. Initially, we considered channels and their surrounding matrices as separate treatment units, and thus sampled from six treatment units per block.

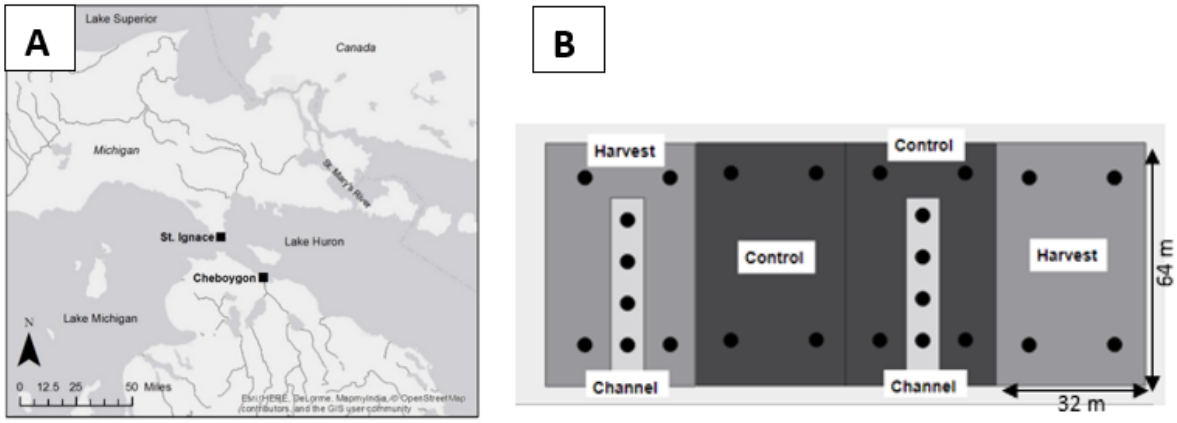


Figure 1. A) Wetland complex locations in the northern Laurentian Great Lakes. We established two experimental blocks at St. Ignace, and one block at Cheboygan. B) Example treatment block. Each block covered an area of 0.82 ha, and channels were 8 m x 48 m down the middle of plot, on the lakeward edge. Black dots indicate sampling points (four per treatment unit).

In summer 2017, we established four sampling points in each of the six treatment units (Fig. 1B). In vegetated treatment units (harvest, control, and matrices), these points were located ~17 m diagonally (45°) from the four plot corners to minimize edge effects, with a minimum distance of 6 m from adjacent treatments. In aquatic channels, sampling points were equidistant from each other along a transect in the middle of channel, with the first and last points approximately 10 m from the plot edge and inward edge of each channel.

Aboveground structure- To quantify aboveground biomass, we counted *Typha* stems and measured *Typha* heights (from soil surface to top of plant) in 1 m x1 m quadrats randomly placed at each sampling point. We used an allometric equation (previously determined from Cheboygan marsh; S. Lishawa, unpublished data) that relates *Typha* height to biomass in order to estimate dry biomass (g/m^2). At each sampling point, we measured photosynthetically active radiation (PAR) with quantum sensors (Li-Cor LI-189 for above water, and Li-Cor LI-250 A for below water) and water depth using a meter stick. We measured PAR above the *Typha* canopy at 2.6 m

above the soil surface, at the water surface, at 5 cm below water surface, and at the soil surface to calculate light transmission curves.

Belowground biogeochemistry- To assess treatment effects on belowground properties and processes (i.e., soil parameters, belowground biomass, discrete nutrient concentrations, and carbon mineralization rates), we collected soil samples (5 cm diameter to 10 cm depth) from three to four sampling points per treatment unit (Fig. 1B) and composited them in the field. We collected three bags of composited samples per plot, and transported cores on ice to the laboratory (University of Michigan Biological Station). One bag of soil was immediately processed for bulk density, one bag was frozen (-18°C) until root analysis, and one bag was stored at 4°C for < two weeks and passed through a 2-mm sieve before further processing.

Physical soil parameters- Subsamples of 2-mm sieved soils were dried at 105 ºC for 48 hours to determine soil water content, and soil moisture was calculated by dividing soil water content by dry soil weight. The subsamples were pulverized and stored in a desiccator until analytical triplicates were analyzed for C and N content using a Costech 4010 Elemental Analyzer. We estimated bulk density (g/cm^3) on un-sieved samples that were dried (105ºC for 48 hours) and weighed per unit volume.

Soil respiration- To quantify soil respiration rates, we used a static soil incubation method adapted from Fierer et al. (2003). Composited samples were passed through a 2-mm sieve to remove rhizomes and large roots, and soil respiration rates were quantified within two weeks of collection. We weighed three analytical replicates (~50 g soil) of each field-moist soil sample into glass canning jars (0.95 L), let the jars sit for ~2 hours until soil temperature was ~25ºC, and then attached the incubation jars to a real-time isotopic gas analyzer (Picarro G2201-i) via a 15-port rotary-valve manifold. Incubations were kept dark with an opaque tarp.

Because the manifold creates a closed loop, we ran a soda lime CO_2-free blank for four minutes at the beginning of each jar incubation to displace the previous sample from the line and avoid cross contamination between samples; thus the headspace of each incubation replicate was exposed to CO_2-free air and atmospheric concentrations of CH_4. The headspace was then sampled for eight minutes during which the concentration came to steady state (i.e., leveled off) once the closed loop was re-circulating headspace air. We used steady state concentrations at time 0, 3, 6, and 24 hours to calculate the rate of linear gas concentration change in the jar's headspace over time.

We processed data in R (version 3.1.4) using original code in order to extract the data from Picarro files, identify steady state concentrations, and calculate concentration changes and flux rates. All linear rates were within the minimal detectable concentration differences (0.001 ppm for CO_2 and 3.3 x 10^{-6} ppm for CH_4) for our instrument. Using code adapted from S. Moseman-Valtierra and R. Martin (personal communication), we converted linear concentration change rates from volume/volume/time (ppm/s) to mass/volume/time (umol/s) by applying the ideal gas law using the jar volume, room temperature measurements (per minute by I-buttons, Maxim Integrated, USA), and standard atmospheric pressure (1 atm). Grams of dry soil in each jar were calculated using the field moist weight and soil moisture measurements of each sample, and then converted to grams of soil carbon using C content values from our soil C:N analysis. We calculated flux rates as the headspace linear concentration change per gram of soil carbon, because we were interested specifically in microbial activity in terms of carbon turnover.

Soil pore water nitrogen concentrations- Subsamples of 2-mm sieved soils were centrifuged, and their soil water was filtered (Whatman cellulose, 45 nm) and frozen (-18ºC) until NH_4-N and NO_x-N analysis. Soil water samples were thawed, and analyzed for ammonium nitrogen (NH_4-N;

EPA method 350.1) and nitrate + nitrite nitrogen (NOx-N; EPA method 353.2) using a SmartChem 200 discrete analyzer at the University of Connecticut. Check standards were run every 10 samples, and percent error was less than 22% on all check standards. Analytical duplicates were run every 20 samples. All concentrations were above the instrument's detection limit (0.085 mg/L for NH_4-N and 0.047 mg/L for NO_x-N).

In-situ soil nutrient availability- To measure soil availability rates of plant-available ions, we installed Plant Root Simulator (PRS) probes (©Western Ag, Canada) at all four sampling points within each treatment unit for two weeks. PRS probes are ion exchange membranes (surface area = 10 cm^2) surrounded by plastic casing designed for field deployment. Over the course of a burial period, anions continuously adsorb to probes pre-treated with bicarbonate (HCO_3^-) and cations adsorb to probes pre-treated with sodium (Na^+). PRS probes at two plots were not recovered (St. Ignace East; channel surrounded by harvest, and harvested matrix). Post-collection, we cleaned the probes of debris using de-ionized water and a brush, stored them at 4ºC, and shipped them cold to Western Ag. The PRS probes were eluted with 0.5 N HCl for one hour to desorb ions from the ion-exchange membrane (Hangs et al. 2004). The eluent was analyzed for NH_4-N and NOx-N using calorimetry (Skalar Continuous Flow Analyzer). Analyses of phosphorus (P), manganese (Mn), iron (Fe), potassium (K), and calcium (Ca) were completed using inductively coupled plasma optical emission spectrometry (Perkin Elmer ICP-OES 8300). For all analyses, Western Ag ran a standard curve for each batch of samples, and ran control samples every 20 samples.

Belowground biomass- To quantify root mass and length, frozen composited soils were thawed and washed over a 1-mm sieve, through which mineral and organic soil material passed. The remaining sample consisted of live roots, rhizomes, and macro-organic matter (i.e., partially

decomposed roots, leaf litter debris >1mm in size). We separated rhizomes and then on approximately 1/8th of the remaining sample, separated roots from macro-organic matter and scanned the roots to estimate root length using the Smart Root plug-in within Image J. All biomass was dried at 65°C (≥ 72 hours). We scaled our root mass, root length, and macro-organic matter estimates to the entire sample, and used the composite sample volume to standardize mass or length per unit volume.

Data Analysis- For all analytical triplicates (soil respiration rates, moisture, C: N, and aqueous discrete nutrient concentrations), we omitted any value that was not within 20% of the other two replicates, and averaged the replicates for each treatment at each block. We used linear mixed effects regression (*lmertest* package in R version 3.4.1) analyses to test how management treatments affected *Typha* biomass, soil respiration, and soil nutrient availability. Given the variation across blocks, we included block as a random factor to distinguish this variation from random error (McCulloch et al. 2008). We also accounted for relevant environmental parameters in our analyses; we included water depth as a covariate in aboveground biomass analysis, standardized soil respiration rates by soil carbon, and included soil moisture as a covariate in analysis of nutrient availability. We tested for normality using the Shapiro-Wilks test, checked for heteroscedasticity by plotting residuals against fitted values, and log 10-transformed data to meet model assumptions when necessary. Preliminary analysis suggested no difference between the treated matrices (harvest and control) versus whole plots, nor between the two channels. In order to more explicitly identify effects of harvested stands and channels relative to *Typha*-dominated control stands, we aggregated the treatments to harvest (harvested plot and harvested matrix), channel (channel surrounded by harvested matrix and channel surrounded by control matrix), and control (control plot and control matrix). Because we were specifically interested in

how restoration treatments compared to un-manipulated reference stands (not necessarily how channel compares to harvest), we used the *lmertest* summary function, which calculates t-tests between control and each respective treatment using Satterthwaite approximations for degrees of freedom. We assessed significance at $p \leq 0.05$. All treatment means are presented ± 1 standard error (SE).

Results

Site characteristics- Soils at all experimental blocks were organic with low bulk density. Since lake levels were high compared to long-term average values (Gronewold et al. 2015), surface water depths at our blocks were all ~ 50 cm (Table 1).

Table 1. Block averages ± SE of soil and surface water properties, n = 6 per site.

	Soil				Surface Water Depth (cm)
	% C	% N	% Moisture	Bulk Density (g/cm^3)	
Cheboygan	21.40 ± 2.09	1.26 ± 0.13	81 ± 2	0.27 ± 0.04	57.7 ± 4.0
St. Ignace East	23.02 ± 1.03	1.32 ± 0.06	83 ± 1	0.26 ± 0.01	49.6 ± 1.0
St. Ignace West	20.38 ± 1.15	1.13 ± 0.09	79 ± 2	0.28 ± 0.03	46.6 ± 0.6

Aboveground structural metrics- One year following harvest of *Typha* ~ 20 cm above the water surface, *Typha* re-grew with higher density ($t_{12} = 2.2$, $p = 0.05$), but slightly less aboveground stem biomass ($t_{12} = -1.9$, $p = 0.08$) relative to un-manipulated control stands (Table 2). *Typha* stem biomass remained largely absent from channels ($t_{13} = -6.28$, $p < 0.001$) that had been creating using weedwackers at the soil surface.

Table 2. Treatment averages ± SE of *Typha* aboveground metrics, n = 6 per treatment. (***** indicates manipulated stand of *Typha* was different from un-manipulated control)

	Height (m)	Density (#stems/m^2)	Stem Biomass (g/m^2)
Control	1.92 ± 0.23	29 ± 4	692.8 ± 110.3
Harvest	1.87 ± 0.04	38 ± 4*****	507.1 ± 91.9
Channel	0.07 ± 0.07*****	0.04 ± 0.04*****	0.4 ± 0.4*****

The change in aboveground biomass among treatments altered patterns of light transmission; almost half of the available light was intercepted by the aboveground vegetation in control and harvested stands, while the greatest light reduction in the channels occurred in the water column (Fig. 2). Harvested stands and open-water channels each had significantly more light transmittance to the water surface than the un-manipulated control stands (harvest: $t_8 = 7.4$, $p < 0.001$, channel: $t_8 = 16.1$, $p < 0.001$), likely due to removal of standing detritus with harvest, and due to lack of *Typha* stem biomass in channels. Ultimately, harvested stands and control stands had a similar amount of light reach the soil surface, while a greater percentage of available light reached the soil surface in the channels than in controls (harvest: $t_9 = 1.72$, $p = 0.1$; channel: $t_9 = 6.40$, $p < 0.001$).

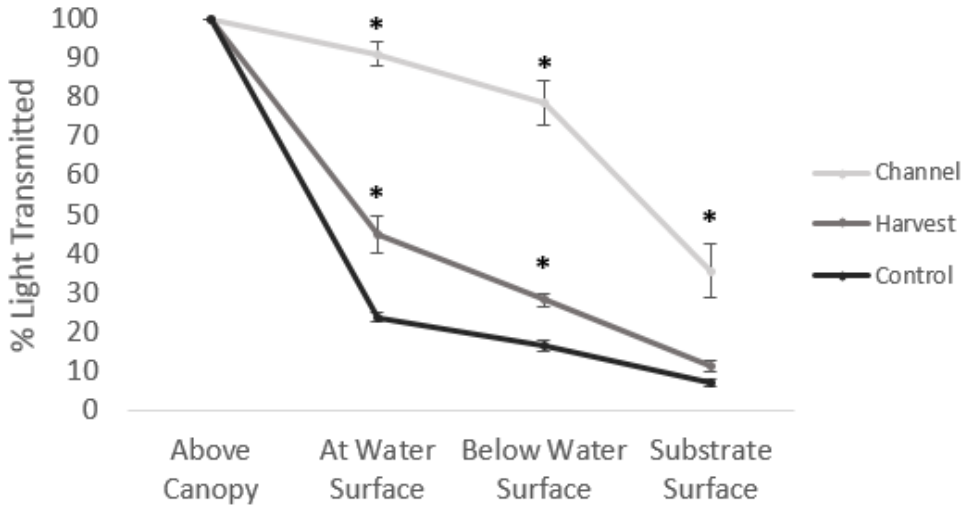


Figure 2. Light transmission through vertical profiles for each treatment (mean ± SE). Above canopy: 2.6 m above substrate surface. Data from St. Ignace East and St. Ignace West (n = 4 for each treatment). Data were log-10 transformed for statistical analysis. (For each profile level, * indicates % light transmitted in manipulated stand of *Typha* was different from un-manipulated control)

Belowground biomass- Contrary to our hypothesis, treatments did not alter root (harvest: $t_{13} = -0.45$, $p = 0.66$, channel: $t_{13} = -0.53$, $p = 0.60$) or rhizome biomass (harvest: $t_{13} = 1.16$, $p = 0.27$, channel: $t_{13} = 1.80$, $p = 0.09$) relative to un-manipulated control stands (Table 3). Channels increased the density of macro-organic matter (>1 mm) relative to un-manipulated controls (harvest: $t_{13} = 1.03$, $p = 0.32$, channel: $t_{13}=3.15$, $p = 0.008$). There were no treatment differences in root length (harvest: $t_{13} = 0.13$, $p = 0.9$, channel: $t_{1\,3}= -1.18$, $p = 0.3$), as there were roots present in the channel soil, consisting of live roots of submerged vegetation or *Typha* roots that had not yet decomposed.

Table 3. Belowground biomass components across treatments (mean ± SE; n = 6 per treatment). (***** indicates treated *Typha* stand differed from un-manipulated control)

	Belowground Biomass (mg/cm^3)			**Root length (cm/cm^3)**
	roots	**rhizomes**	**macro-organic matter**	
Control	2.47 ± 0.25	4.50 ± 0.4	17.58 ± 2.1	2.05 ± 0.28
Harvest	2.27 ± 0.19	7.32 ± 1.49	19.51 ± 2.88	2.09 ± 0.17
Channel	2.05 ± 0.42	8.90 ± 3.17	23.50 ± 1.43*****	1.60 ± 0.42

Soil respiration- We had predicted removal of vegetation would decrease carbon exudates to the soil and decrease soil respiration rates relative to un-manipulated controls, but we found no significant treatment effects on CO_2 production (harvest: $t_{14} = 0.89$, $p = 0.39$, channel: $t_{14} = 0.29$, $p = 0.77$). Harvest and control soils had median values of 42.20 and 39.65 ug C-CO_2/g soil C/hr respectively, while median soil CO_2 production from channels was 30.03 ug C-CO_2/g soil C/hr, (Fig. 3A). We observed soil CH_4 production that ranged from 0.089 to 15.75 ug C-CH_4/g soil C/hr (Fig. 3B). Neither harvesting ($t_{12} = 1.95$, $p = 0.08$) nor channel creation ($t_{13} = 1.02$, $p = 0.33$) significantly shifted soil CH_4 production relative to controls.

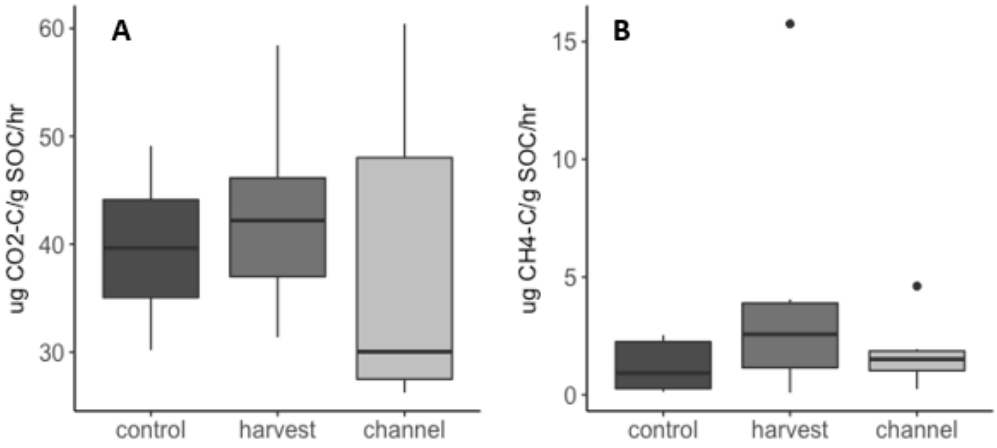


Figure 3. Boxplots of soil A) CO_2 production and B) CH_4 production per gram of soil organic carbon per hour, n = 6 per treatment. CH_4 data were log-10 transformed for statistical analysis.

While treatments did not strongly influence root properties or soil respiration rates, we examined how these plant and soil parameters were related to each other. Linear mixed regression indicated soil CO_2 production was not related to root biomass ($p = 0.32$) or root length ($p = 0.81$). Likewise, neither *Typha* stem biomass ($p = 0.84$) nor soil macro-organic matter ($p = 0.96$) were related to soil CO_2 production. CH_4 production was not related to root biomass ($p = 0.66$) or *Typha* stem biomass ($p = 0.55$). There was a slight trend (Appendix I; $p \sim 0.1$) of decreased CH_4 production with increased root length ($p = 0.13$), and soil CH_4 production slightly trended toward decreased rates in soils that had more macro-organic matter ($p = 0.10$).

Soil water nitrogen- Harvested *Typha* stands had increased nitrate + nitrite (NO_x-N) concentrations relative to un-manipulated controls (Fig. 4A; harvest: $t_{14} = 3.17$, $p = 0.007$, channel: $t_{13} = -0.04$, $p = 1.0$), but concentrations of ammonia (NH_4-N) did not differ one year after harvest and channel creation (Fig. 4B; harvest: $t_{11} = -1.5$, $p = 0.2$, channel: $t_{11} = -1.25$, $p = 0.2$). For plant-available N measured using PRS probes, soil NO_x-N availability rates were all below detection limit, and NH_4-N availability rates were not affected by treatment (Table 4).

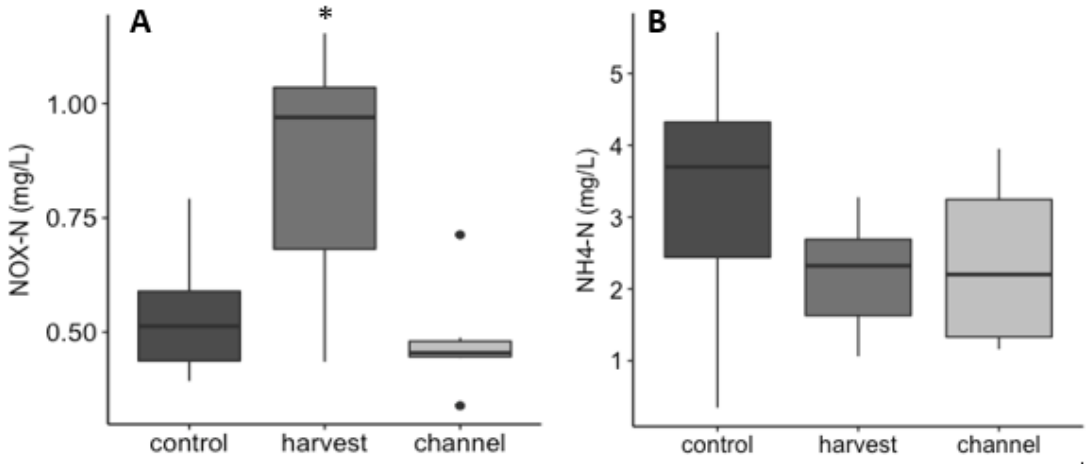


Figure 4. Boxplots of A) concentrations of soil water nitrate + nitrite (NOX-N), and B) concentrations of soil water ammonia (NH4-N), n = 6 per treatment. (* indicates manipulated stand of *Typha* was different from un-manipulated control.)

Soil nutrient availability rates- While there were minimal effects on soil water nitrogen, management treatment of invasive *Typha* did affect nutrient availability rates of other soil nutrients (Table 4). Channel creation increased availability rates of phosphorus (P) and potassium (K) relative to un-manipulated control stands, though other plant macronutrients (Ca, Mg, S) were not affected by treatment (Table 4). Rates of manganese (Mn) availability were lower in channels relative to un-manipulated controls, and other redox-active ions (Fe, S) were not affected by experimental treatment.

To determine if nutrient availability was related to *Typha* biomass, we used linear mixed regression. Plant available P and K decreased as *Typha* aboveground biomass increased (Fig. 5A; $p = 0.04$, Fig 5B; $p = 0.015$). Plant available K also increased as soil macro organic matter mass increased ($p = 0.03$). Unlike P and K, *Typha* aboveground biomass did not affect Mn ($p > 0.5$), and Mn decreased as macro-organic matter increased ($p = 0.04$).

Table 4. Treatment averages of nutrient availability rates (ug/10cm^2/14 days) measured by PRS ion exchange membranes, n=6 for control, n=5 for harvest and channel, due to missing probes in two plots at St. Ignace East. (* indicates manipulated stand of *Typha* was different from un-manipulated control.)

	Control	Harvest			Channel		
	mean ± SE	mean ± SE	t	p-value	mean ± SE	t	p-value
NH_4-N	3.32 ± 1.02	3.35 ± 0.41	0.21	0.84	3.34 ± 0.66	0.25	0.81
K	10.67 ± 2.21	10.42 ± 0.61	0.00	1.00	18.17 ± 2.45	3.30	0.01*
Ca	2,190.01 ± 35.24	2,291.48 ± 112.42	0.88	0.39	2,162.33 ± 66.70	-0.27	0.79
Mg	347.99 ± 21.36	334.71 ± 29.15	-0.97	0.36	348.49 ± 22.46	-0.30	0.77
P	3.49 ± 1.20	2.80 ± 0.67	-1.02	0.33	5.88 ± 1.11	3.79	0.00*
S	12.34 ± 1.28	12.54 ± 1.67	0.23	0.83	15.34 ± 2.50	1.44	0.18
Fe	661.32 ± 83.75	677.46 ± 43.06	0.48	0.64	679.69 ± 50.79	0.61	0.55
Mn	10.24± 4.46	8.03 ± 2.60	-1.12	0.29	5.06 ± 1.07	-2.44	0.03*

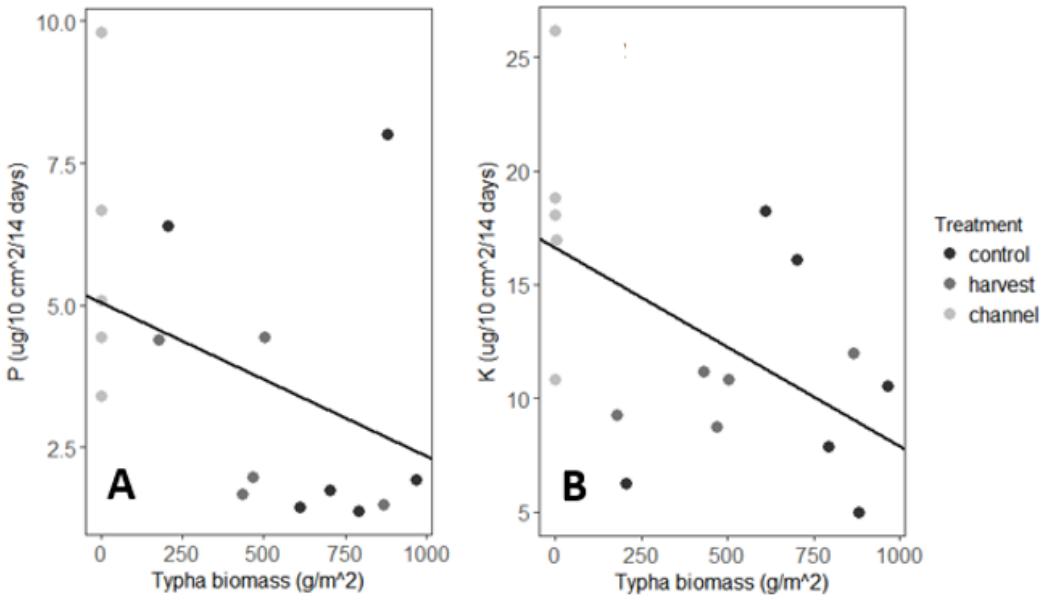


Figure 5. Linear mixed effects regression indicated that both A) phosphorous (P) and B) potassium (K) decreased with *Typha* aboveground stem biomass. Points are colored according to treatment, regressions analyzed the entire data set (n=16).

To determine if nutrients affected soil respiration rates, we used linear mixed regressions. Concentrations of N species did not affect CO_2 production ($p > 0.05$). However, as discrete concentrations of NH_4-N increased, soil CH_4 production decreased ($p = 0.009$), and there was a

slight trend at $p < 0.1$ indicating as discrete concentrations of NO_x-N increased, soil CH_4 production increased ($p = 0.08$). Finally, we found that Fe availability rates strongly and positively explained rates of soil production of CO_2 and CH_4 (Fig. 6A; $p = 0.002$, Fig. 6B; $p = 0.02$).

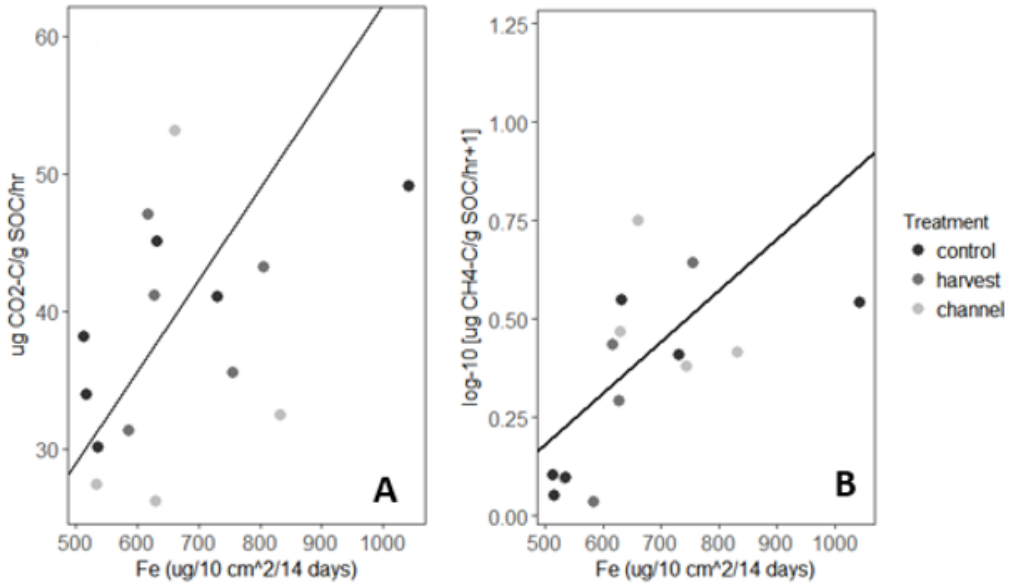


Figure 6. Linear mixed effects regression indicating how soil iron availability affects soil respiration rates of A) carbon dioxide and B) methane. Points are colored according to treatment, regressions analyzed the entire data set (n=16).

Discussion

Our study of plant-soil responses to *Typha* management suggests that mechanical treatment of dominant clonal graminoids can alter aboveground structure and increase soil availability of plant nutrients. Other belowground properties and processes, such as root biomass and soil respiration rates, may be indirectly affected by channel creation and harvest at the spatial and temporal scales of these treatments.

Light transmission measurements mirrored patterns in aboveground biomass; channels and harvested stands each had less shoot biomass and more light penetration than un-manipulated reference stands. These aboveground structural responses aligned with our expectations, as similar experiments in the region also found *Typha* re-growth one season after mowing and biomass removal, and greater reduction of *Typha* dominance when cut shoots were flooded (Lishawa et al. 2015, Schummer et al. 2012, Hall & Zedler 2010). Cutting *Typha* below the water for channel creation effectively prevented re-growth from stems in the present study, and may be an appealing strategy to immediately reduce invasive species. However, this technique is labor- and time-intensive and unfeasible at large scales, due to the use of hand-held aquatic weedwackers versus a large tracked-vehicle harvester. Harvesting decreased aboveground *Typha* biomass one year after treatment, suggesting that removal of photosynthetic tissue during the peak of the growing season may decrease plant vigor over time and possibly shift resource allocation (Elgersma et al. 2015, Asaeda et al. 2008). Further, mechanical management disrupted biomass/litter accumulation, a structural feedback by which invasive plants maintain dominance (Holdredge and Bertness 2010), and increased light transmission could lead to increased native plant diversity (Keyport et al. *in press*). As water depth was ~0.5 m at our sites, increased light transmission is likely to affect submerged aquatic species and water column phytoplankton, rather than promote native wetland macrophytes, which cannot germinate in extended flooded conditions (Lishawa et al. 2015, Boers et al. 2007).

Roots constitute key biological and structural components of soil carbon and nutrient cycling, and their biomass and length can be a proxy for oxygen availability and carbon exudates in the rhizosphere (Grosse et al. 1996, Welsch & Yavitt 2007). Our belowground biomass results were surprising, because we expected decreased root biomass and length in channels relative to

the *Typha*-dominated controls. The notable variation in belowground biomass may be due to the heterogeneity of dense, *Typha* root networks. Our results also highlight a potential temporal limitation of our investigation, as the well-established *Typha* roots may not have broken down within one year**.** Still, increased macro-organic matter in channels relative to control stands is evidence for slower break down of plant material when management removes the plant conduit (*Typha* stem) between atmosphere and rhizosphere. Thus, soil organic matter and plant litter may constitute a greater link between plant and soil processes than root exudates (Williams & Yavitt 2010, Welsch & Yavitt 2007).

Complete removal of aboveground *Typha* via channel creation led to increased soil water availability of two plant macronutrients (P, K) and decreased availability of one micronutrient that is also redox-active (Mn). P and K availability decreased as biomass increased, and it is likely that reduced cover of macrophytic vegetation led to increased soil availability of two primary nutrients required for protein growth (P) and photosynthesis (K) (Tucker 1999, Lawrence et al. 2016). Mn activates an enzyme that catalyzes plant assimilation of nitrogen (Tucker 1999), and was more available in vegetated control stands than in channels. Mn availability rates were not strongly explained by *Typha* shoot biomass, as Mn is needed for plant growth in smaller amounts than P and K. Assuming increased macro-organic matter indicates slower rates of decomposition, then the link between decreased Mn availability rates in channels and increased soil macro-organic in channels is reasonable because reduction of Mn depends on fermentation byproducts (Laanbroek 1990).

NH_4-N and NO_X-N are particularly dynamic in wetland systems, as these substrates are important for many plant and soil processes. The elevated NO_X-N concentrations in soil pore water of harvested stands potentially indicate increased O_2 availability in the rhizosphere of

harvested stands (possibly stimulated by aggressive re-growth leading to rhizosphere priming; Dijkstra et al. 2013). Non-detectable *in-situ* NO_X-N availability rates were expected given the overall anoxic conditions of wetland soil, because nitrification requires oxygen. Thus, our NO_X-N results highlight how discrete concentrations and *in-situ* availability rate measurements can complement each other to understand plant-soil dynamics.

There is growing evidence that Fe availability can increase wetland CH_4 emissions (Murray et al. 2017, Dinsmore et al. 2017), and Fe availability rates were positively correlated with soil production of CO_2 and CH_4 in the present study. Our results suggest that while cutting macrophyte stems may not directly affect Fe availability (Keller et al. 2013), Fe can be a proxy for availability of oxygen and carbon in rhizosphere soil (Riedel et al. 2013, Neubauer et al. 2007, Keller et al. 2013). PRS probes measure total elemental Fe, but we can reasonably infer that the Fe adsorbed to the membranes was the more mobile, water-soluble Fe (II) that dominates under anoxic conditions. $Fe(OH)_3$ binds to organic matter as it precipitates via oxidation, and the organic matter retained by this plaque is mostly vascular plant-derived root exudates (Riedel et al. 2013), so more water-soluble Fe may indicate less Fe plaque and greater availability of low-molecular weight carbon compounds. While root biomass has been positively correlated with $Fe(OH)_3$ formation by others (Neubauer et al. 2007, Keller et al. 2013), we found no relationship between root biomass nor length with Fe availability. It is worth noting our soil incubations were exposed to atmospheric concentrations of oxygen before each measurement (four minute soda lime blank). *In-situ* patterns of completely anoxic CH_4 production may be greater in magnitude than our lab incubations, or *in-situ* oxygenation of CH_4 by root-filled soil may lead to patterns our observations during lab incubations.

Our results integrate understanding of plant-soil feedbacks with large-scale mechanical management efforts, and contributes to a well-rounded assessment of management outcomes. The increase of plant-available P and K in soil water with channel creation is noteworthy; it would be interesting to investigate whether surface water follows this same pattern, which could indicate whether nutrients are internally cycled or are potentially exported to coastal waters. Likewise, longer-term observations of root and litter decomposition will be important, as these processes could lead to increased greenhouse gas emissions. At the same time, lack of direct treatment patterns in rhizosphere properties and processes may indicated belowground processes re-equilibrate post-treatment, and continued study is necessary to assess whether this new state complements or counteracts aboveground benefits of mechanical management techniques.

References

Asaeda, T, Sharma, P, & Rajapakse, L (2008) Seasonal patterns of carbohydrate translocation and synthesis of structural carbon components in *Typha angustifolia*. *Hydrobiologia* 607 (1): 87-101

Barak, P (1999) Essential elements for plant growth. soils.wisc.edu. After E. Epstein (1965) "Mineral metabolism" pp. 438-466 in: *Plant Biochemistry* (J. Bonner and J.E. Varner, eds.) Academic Press, London, UK. Retrieved from: https://soils.wisc.edu/facstaff/barak/soilscience326/macronut.htm

Boers, AM, Veltman, RLD, & Zedler, JB (2007) *Typha x glauca* dominance and extended hydroperiod constrain restoration of wetland diversity *Ecological Engineering* 29 (3): 232-244

Cowardin, LM, Carter, V, Golet, FC, & LaRoe, ET (1979) *Classification of wetlands and deepwater habitats of the United States*. US Department of the Interior, US Fish and Wildlife Service

Dijkstra, FA, Carrillo, Y, Pendall, E, & Morgan, JA (2013) Rhizosphere priming: A nutrient perspective. *Frontiers in Microbiology* 4:1-8

Dinsmore, K, Drewer, J, Levy, P, George, C, Lohila, A, Aurela, M, & Skiba, U (2017) Growing season methane and nitrous oxide static chamber fluxes from Sodankylä region, Northern Finland. *Biogeosciences* 14: 799-815

Ehrenfeld, JG (2010) Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution, and Systematics* 41: 59-80

Ehrenfeld, JG, Ravit, B, & Elgersma, K (2005) Feedback in the plant-soil system. *Annual Review of Environment and Resources* 30: 75-115

Elgersma, KJ, Wildova, R, Martina, JP, Currie, WS, & Goldberg, DE (2015) Does clonal resource translocation relate to invasiveness of *Typha* taxa? Results from a common garden experiment. *Aquatic Botany* 126: 48-53

Fierer, NA, Andrew S, Schimel, JP, & Holden, PA (2003) Controls on microbial CO_2 production: A comparison of surface and subsurface soil horizons. *Global Change Biology* 9: 1322-1332

Frieswyk, CB & Zedler, JB (2007) Vegetation change in Great Lakes coastal wetlands: deviation from the historical cycle. *Journal of Great Lakes Research* 33 (2): 366-380

Galatowitsch, SM, Anderson, NO, & Ascher, PD (1999) Invasiveness in wetland plants in temperate North America. *Wetlands* 19 (4): 733-755

Gronewold, A, Clites, A, Bruxer, J, Kompoltowicz, KW, Smith, JP, Hunter, TS, & Wong, C (2015) Great Lakes water levels. *EOS Magazine* 96 (6): 14-17

Grosse, W, Armstrong, J, & Armstrong, W (1996) A history of pressurised gas-flow studies in plants. *Aquatic Botany* 54: 87-100

Hall, S & Zedler, J (2010) Constraints on sedge meadow self-restoration in urban wetlands. *Restoration Ecology* 18 (5): 671-680

Hangs, RD, Greer, KJ, & Sulewski, CA (2004) The effect of interspecific competition on conifer seedling growth and nitrogen availability measured using ion-exchange membranes. *Canadian Journal of Forest Research* 34: 754-761

Holdredge, C & Bertness, MD (2010) Litter legacy increase the competitive advantage of invasive *Phragmites australis* in New England wetlands. *Biological Invasions* 13: 423-433

Jakubowski, AR, Casler, M & Jackson, RD (2010) The benefits of harvesting wetland invaders for cellulosic biofuel: an ecosystem services perspective. *Restoration Ecology* 18: 789-795

Keller, J, Sutton-Grier, A, Bullock, A, & Megonigal, J (2013) Anaerobic metabolism in tidal freshwater wetlands:I. Plant removal effects on iron reduction and methanogenisis. *Estuaries and Coasts* 36: 457-470

Keyport, S, Carson, BD, Johnson, O, Lawrence, BA, Lishawa, SC ,Tuchman, NC, & Kelly, JJ (2018) Effects of experimental harvesting of an invasive hybrid cattail on wetland structure and function. *Restoration Ecology* accepted July 7, 2018

Laanbroek, HJ (1990) Bacterial cycling of minerals that affect plant growth in waterlogged soils: a review. *Aquatic Botany* 38 (1): 109-125

Lawrence, BA, Lishawa, SC, Rodriguez, Y, Tuchman, NC (2016) Herbicide management of invasive cattail (*Typha × glauca*) increases pore water nutrient concentrations. *Wetlands Ecology and Management* 24 (4): 457-467

Lishawa, SC, Lawrence, BA, Albert, DA, & Tuchman, NC (2015) Biomass harvest of invasive *Typha* promotes plant diversity in a Great Lakes coastal wetland. *Restoration Ecology,* 23(3): 228-237.

Martin, JL & Blossey, B (2013) The Runaway Weed: Costs and failures of *Phragmites australis* management in the USA. *Estuaries and Coasts* 36: 626-632

McCulloch, CE, Searle, SE & Neuhas, JM (2008) "Linear mixed effects models", pp. 309-358 in: *Wiley Series in Probability and Statistics Series: Generalized, Linear, & Mixed*

Models (C.E. McCulloch, S.R. Searle, & J.M. Neuhas) John Wiley & Sons, Inc. Hoboken, New Jersey, USA

Murray, K, Barlow, N, & Strack, M (2017) Methane emissions dynamics from a constructed fen and reference sites in the Athabasca Oil Sands Region, Alberta. *Science of the Total Environment* 583: 369-381

Neubauer S, Toledo-Durán, G, Emerson, D, & Megonigal, J (2007) Returning to their roots: Iron-oxidizing bacteria enhance short-term plaque formation in the wetland-plant rhizosphere. *Geomicrobiology Journal* 24 (1): 65-73

Paterson, E (2003) Importance of rhizodeposition in the coupling of plant and microbial productivity. *European Journal of Soil Science* 54: 741-750

Peralta, AL, Muscarella, ME, & Matthews, JW (2018) Wetland management strategies lead to tradeoffs in ecological structure and function. *Elementa Science of the Anthropocene* 5: 74

Petersen, JE, Kemp, WM, Bartleson, R, Boynton, WR, Chen, C, Cornwell, JC, Gardner, RH, Hinkle, DC, Houde, ED, Malone, TC, Mowitt, WP, Murray, L, Sanford, LP, Stevenson, JC, Sundberg, KL, & Suttles, SE (2003) Multiscale experiments in coastal ecology: improving realism and advancing theory. *BioScience* 53 (12): 1181-1197

Riedel, T, Zak, D, Biester, H, & Dittmar, T (2013) Iron traps terrestrially derived dissolved organic matter at redox interfaces. *PNAS* 110 (25): 10101-10105

R version 3.4.1 (2017-06-30) -- "Single Candle", Copyright (C) 2017 The R Foundation for Statistical Computing, Platform: x86_64-w64-mingw32/x64 (64-bit)

Schummer, ML, Palframan, J, McNaughton, E, Barney, T, & Petrie, SA (2012) Comparisons of bird, aquatic macroinvertebrate, and plant communities among dredged ponds and natural wetland habitats at Long Point, Lake Erie, Ontario. *Wetlands* 32: 945-953

Tucker, RM (1999) Essential plant nutrients. carteret.ces.ncsu.edu. Agronomic Division, North Carolina Department of Agriculure and Consumer Services. Retrieved from: https://carteret.ces.ncsu.edu/files/library/16/2%20Essential%20Plant%20Nutrients.pdf

Welsch, M & Yavitt, J (2007) Microbial CO_2 production, CH_4 dynamics and nitrogen in a wetland soil (New York State, USA) associated with three plant species (*Typha, Lythrum, Phalaris*) *European Journal of Soil Science* 58 (6): 1493-1505

Williams, C, & Yavitt, J (2010) Temperate Wetland Methanogenesis: The Importance of Vegetation Type and Root Ethanol Production. *Soil Science Society of America Journal* 74 (1): 317-325

Zedler, J & Kercher, S (2005) Wetland resources: status, trends, ecosystem services, and restorability. Annual Review of Environment and Resources 30: 39-74